COMPARATIVE LIFE HISTORIES AND STOCK ASSESSMENTS OF ROCKCODS (FAMILY SERRANIDAE) FROM THE EAST COAST OF SOUTH AFRICA.

by

Sean Thomas Fennessy

Submitted in fulfillment of the academic requirements for the degree of Doctor of Philosophy in the School of Life and Environmental Sciences, University of Natal, Durban.

December 2000

ABSTRACT

The family Serranidae is a diverse group of fishes, of which the genus *Epinephelus* (rockcods or groupers) is the largest. Serranids are commonly caught in reef fisheries in tropical and warm-temperate latitudes, and are targeted because of their tasty flesh and high value. In South Africa, epinepheline serranids mainly occur in hook and line fisheries in the province of KwaZulu-Natal. Most serranids are caught by the boat-based (skiboat) fishery, and the commonest species are the endemic catface rockcod (*Epinephelus andersoni*), the halfmoon rockcod (*E. rivulatus*), the yellowbelly rockcod (*E. marginatus*) and the endemic white-edge rockcod (*E. albomarginatus*). Although serranids contribute about ten percent to catches by the commercial and recreational skiboat sectors in KwaZulu-Natal, representing an estimated total catch of around 200 mt per year, little is known about these fishes in South Africa. From the mid-1980s to the mid-1990s, the mean lengths of *E. marginatus* and *E. albomarginatus* in the region declined significantly. Over this period, lengths of *E. andersoni* remained the same, while those of *E. rivulatus* increased. Lengths of *E. marginatus* and *E. albomarginatus* from Mozambique, where fishing effort was low at the time of sampling, were significantly greater than in KwaZulu-Natal.

Monthly biological data were mostly collected from commercial skiboat catches on the northern and southern coast of KwaZulu-Natal. Additional data for *E. marginatus* and *E. albomarginatus* were also collected irregularly from commercial catches made in Mozambique. Unless the fish had ripe ovaries, all gonads had to be sectioned to establish sex and stage. Histology revealed that all gonads had a female-like appearance, with lamellae and a central lumen. In *E. andersoni*, there was a complete overlap of male and female length frequencies, and their mean lengths were not significantly different. Some males and inactive bisexuals were both smaller and younger than the female size and age at first maturity. Together with the occurrence of mature bisexual fish (transitionals), these observations indicate that males are derived from immature or mature females, hence this species is a diandric protogynous hermaphrodite. The other three species exhibit typical signs of monandric protogynous hermaphroditism. Males and females had significantly different mean lengths, and age and length frequencies by sex were bimodal. Transitional individuals were recorded in *E. rivulatus*.

E. andersoni and *E. rivulatus* matured at small sizes and early ages relative to *E. marginatus* and *E. albomarginatus*. Ripe ovaries were much larger than ripe testes in all four species. *E. andersoni*, *E. marginatus* and *E. albomarginatus* spawned in spring and summer, while *E. rivulatus* spawned in winter and spring. There were no indications of spawning in *E. andersoni* in the southern sampling region, and few ripe individuals of *E. albomarginatus* were encountered in KwaZulu-Natal samples. Size at maturity of this species was much smaller in Mozambique samples. Large, reproductively inactive individuals of *E. andersoni* were frequently observed in the spawning season. The lack of reproductive activity of *E. andersoni* and *E. albomarginatus* in KwaZulu-Natal may be because this area represents the southernmost limit of the distribution of these species.

Ageing of the four species was undertaken using sectioned otoliths. Age validation was undertaken by a combination of tetracycline marking in captive fishes, and analysis of the marginal zone in otoliths. All four species are relatively long-lived, although estimates of maximum age may be under-estimated because of long-term harvesting. In all four species, fish from the southern sampling region were larger than fish from the northern region at the same age. Only in the case of *E. rivulatus* were these significant enough to warrant the fitting of two growth curves to the northern and southern populations. Males in all four species tended to be larger than females at the same age, suggesting that there may be a growth spurt following sex change, or that faster-growing females changed sex. A logistic growth curve was fitted to the age-length data for *E. andersoni*, while von Bertalanffy curves produced the best fit for the other species. Based on the rates at which $L\infty$ is attained in these four species, *E. marginatus* and *E. albomarginatus* are slow-growing species, while *E. andersoni* and, particularly, *E. rivulatus* are faster growing.

Rates of total mortality and natural mortality were estimated using length-converted catch curves and the Rikhter and Efanov equation, respectively. Stock assessments undertaken by yield per recruit and spawner biomass per recruit analyses indicate that *E. andersoni* in KwaZulu-Natal is currently optimally exploited, while *E. rivulatus* is lightly exploited. Both *E. marginatus* and *E. albomarginatus* are over-exploited. The potential problems in applying standard per recruit models to species with complex life histories are discussed. Support for the reduced stock status of the latter two species is provided by the observed changes in lengths of these species over a ten-year period, and their relatively small size in KwaZulu-Natal compared to the lightly-fished Mozambique populations. Local fishers in KwaZulu-Natal have also reported declines in sizes and reduced catches of these two species.

The life history styles and other features of the four species are compared and discussed with reference to the resilience of these species to harvesting. Two of the species (*E. marginatus* and *E. albomarginatus*) are monandric protogynous hermaphrodites, which grow slowly, mature late and attain large sizes. *E. andersoni* and *E. rivulatus* grow faster, mature earlier and are smaller species. The normally deleterious effects of fishing on sex-changing species are not manifested in these two species, possibly because *E. rivulatus* is so small, that males are not selectively removed. In contrast, *E. andersoni* is a diandric protogynous hermaphrodite, and hence, does not rely on sex-change as a source of males. The current management methods for serranids in KwaZulu-Natal are presented, and suggestions for future approaches are discussed.

PREFACE

The work described in this thesis was carried out at the Oceanographic Research Institute in Durban, from January 1999 to December 2000, under the supervision of Dr Lynnath Beckley (Oceanographic Research Institute) and Professor Yvonne Sadovy (University of Hong Kong).

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

ACKNOWLEDGMENTS

Where to begin? Dr Lynnath Beckley and Professor Yvonne Sadovy initially provided me with sufficient courage to begin this process. They then proceeded to support and guide me for the past two years – without them, this research would have remained as a series of dusty reports to management agencies (with perhaps a paper or two). Many thanks to you, Lynnath, for some clear thinking and planning, and to you, Yvonne, for encouraging comments and clearing some hermaphroditic mists.

Research is costly in terms of time and money. The South African Association for Marine Biological Research, incorporating the Oceanographic Research Institute (ORI), provided some of the funds, but more importantly, the time and opportunity for me to do the work and write it up. To the Director, Professor Tony de Freitas, and the Deputy Director, Rudy van der Elst, thank you for this. The KwaZulu-Natal Nature Conservation Service provided a substantial part of the funds for this research. Some of its officers, particularly Kevin Green and Callum Beattie, were of invaluable help in obtaining the necessary information. The National Research Foundation generously provided funds to bring Yvonne Sadovy out to South Africa – this was critical for the description of sexual patterns. The Natal University Research Fund also assisted with the funding of field trips.

To my colleagues at ORI, thank you for your support and good wishes. Derek Arthur, Bruce Mann, Simon Chater and Bryan van der Walt all helped with the collection of samples. Gary and Shelley Birnie also produced some great samples. Several staff at Sea World helped to keep "my" rockcod alive – thanks to John Ballard, Paul Zammit and Andre Bok. Several skippers and fishing companies were exceptionally co-operative in making their catches available to me: Paul Loomes (Tight Lines Fisheries), the late Paul Kolenda (Inyoni Fisheries), Nelson Pillay (Victoria Seafoods), Ewald Fourie, Jannie Nel, Len and Trevor Harvey, Willie Reede, and others – without you and your experience, this work would not have been possible. To Tyrone Ridgeway, Paul de Bruyn and the late Bryce Allen, thank you for your help in the laboratory – I hope you learned as much as I did. To Alke Kruger of ORI, many thanks for your assistance and instruction with the histology procedures. To Elinor Bullen, thank you for the kind wishes and the tagging reports. To Bruce Mann and particularly Anesh Govender of ORI, thank you for your comments on drafts of this thesis; Anesh, stock assessment will never be the same again! Professor Tom Hecht and Robin Cross of Rhodes University kindly allowed me the use of their photographic facilities. James Wesley-Smith of the EM unit, University of Natal helped me with the histological photos at a time when his PhD was hanging heavily on him. Charlene Nell of ORI assisted with assembling of the thesis, and Bernadine Everett produced great photo-plates of the histology and the otoliths, and also printed the first drafts of the thesis. For your help at a stressful time, thank you.

To my parents, who started me on the road to research years ago, thank you for your support. Finally, to my long-suffering wife: to her went the painful jobs of editing the references and looking after me when all seemed lost. Merril, the serranids of KwaZulu-Natal and I salute you!

CONTENTS

CHAPTER 1: INTRODUCTION

The family Serranidae is a diverse group of fishes (about 320 species), comprising four subfamilies of which the Epinephelinae (rockcods or groupers) is the largest (Heemstra and Randall, 1993). The genus *Epinephelus* represents the most speciose, 98 in all. The epinepheline serranids are generally found in shelf waters (less than 200 m), and are well-represented in tropical and warm-temperate latitudes in all three oceans. They are demersal species, and are usually associated with reefs (Huntsman *et al.*, 1999).

Serranids form an important part of the catch of hook and line fisheries (also known as linefisheries), and contributed about 150 000 mt to total world catches in 1996 (FAO, 1998). As reefs are particularly extensive in the Indian Ocean and the western regions of the Atlantic and Pacific Oceans, serranids are often important components in catches from these geographic areas (Table 1.1). The preference of these fishes for warmer waters is reflected in their reduced importance in linefisheries located in higher (> 35°) latitudes (Table 1.1). Thus, linefisheries in South Africa, southern Mozambique and southern Australia all have families other than serranids as their main components.

Table 1.1: Principal teleost families in the catches of linefisheries from the Atlantic, Indian and Pacific oceans. Attention is drawn to the serranids (italicised).

Area	Family	Source
Western Atlantic Ocean		
Gulf of Mexico	Lutjanidae, Carangidae, *Serranidae*, Haemulidae	Huntsman and Waters, 1987
U.S. South Atlantic	Lutjanidae, Carangidae, *Serranidae*, Haemulidae	Huntsman and Waters, 1987
Caribbean	Lutjanidae, Carangidae, *Serranidae*, Haemulidae	Munro (1983)
Western Indian Ocean		
Kenya	Lutjanidae, Lethrinidae, *Serranidae*, Sparidae	Morgans (1964)
Southern Mozambique	Lutjanidae, Sparidae, Lethrinidae	van der Elst *et al.* (1994)
South Africa	Gempylidae, Sparidae, Carangidae, Sciaenidae	Penney *et al.* (1999)
Eastern Indian Ocean		
Western Australia	Sparidae, *Serranidae*, Labridae	Francesconi & Clayton (1996)
Southern Australia	Platycephalidae, Sparidae, Sciaenidae, Arripidae	Longhurst and Pauly (1987)
Indian Ocean islands	Lutjanidae, Lethrinidae, *Serranidae*, Scombridae, Carangidae	Anderson *et al.* (1991), Jennings *et al.* (1995)
Western Pacific Ocean		
South-eastern Australia	Sparidae, Platycephalidae, Carangidae	Steffe and Murphy (1995)
Pacific islands	Lutjanidae, Lethrinidae, *Serranidae*, Carangidae, Labridae	Wright and Richards (1985), Grant (1981)

It is also apparent from catches of serranids reported to the Food and Agriculture Organisation (FAO) of the United Nations (Table 1.2) that the largest catches of serranids are made in lower latitudes. Over the period examined, only 12 of

Table 1.2: Reported world catches (mt) of serranids by FAO fishing areas, for all fishing gears (FAO, 1998). F = FAO estimate from available information.

FAO area	Fishing area	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	Total
27	Northeastern Atlantic	166	278	273	197	237	213	257	F 286	F 221	320 F	1621
31	Central/western Atlantic	24193	26200	26551	29544	26451	22448	23569	26732	23822	20239	249749
34	**Central/eastern Atlantic**	**8913**	**15075**	**F 15114**	**F 15565**	**F 14034**	**F 13877**	**F 14554**	**F 16082**	**F 14473**	**F 11357**	**23988**
37	Mediterranean	F 5930	F 6518	F 7649	F 10062	F 7815	F 8385	F 7917	F 8070	F 7849	F 7315	77510
41	Southwestern Atlantic	6090	F 7497	F 5200	F 5491	F 5466	F 5671	F 5449	F 5459	F 5410	F 5320	57053
47	Southeast Atlantic	219	326	251	300	30	30	57	60	32	48	1353
51	Western Indian	11638	F 11609	13014	15646	15566	F 17321	F 17770	F 21252	F 21824	F 23176	168816
57	Eastern Indian	4957	6135	5290	6529	6728	8055	10776	9048	11149	13033	81700
61	Northwest Pacific	3039	3576	3682	17892	18771	23600	22906	25588	24770	25698	169522
71	Central/western Pacific	15131	19238	16293	16243	19397	23960	28647	39740	31326	35878	245853
77	Central/eastern Pacific	F 908	F 663	F 842	F 886	F 837	F 865	F 2060	F 1539	F 4630	F 7250	20480
87	Southeastern Pacific	58	25	24	18	50	43	16	28	22	43	327
Total		81242	97140	94183	118373	115382	124468	133978	153884	145528	149677	

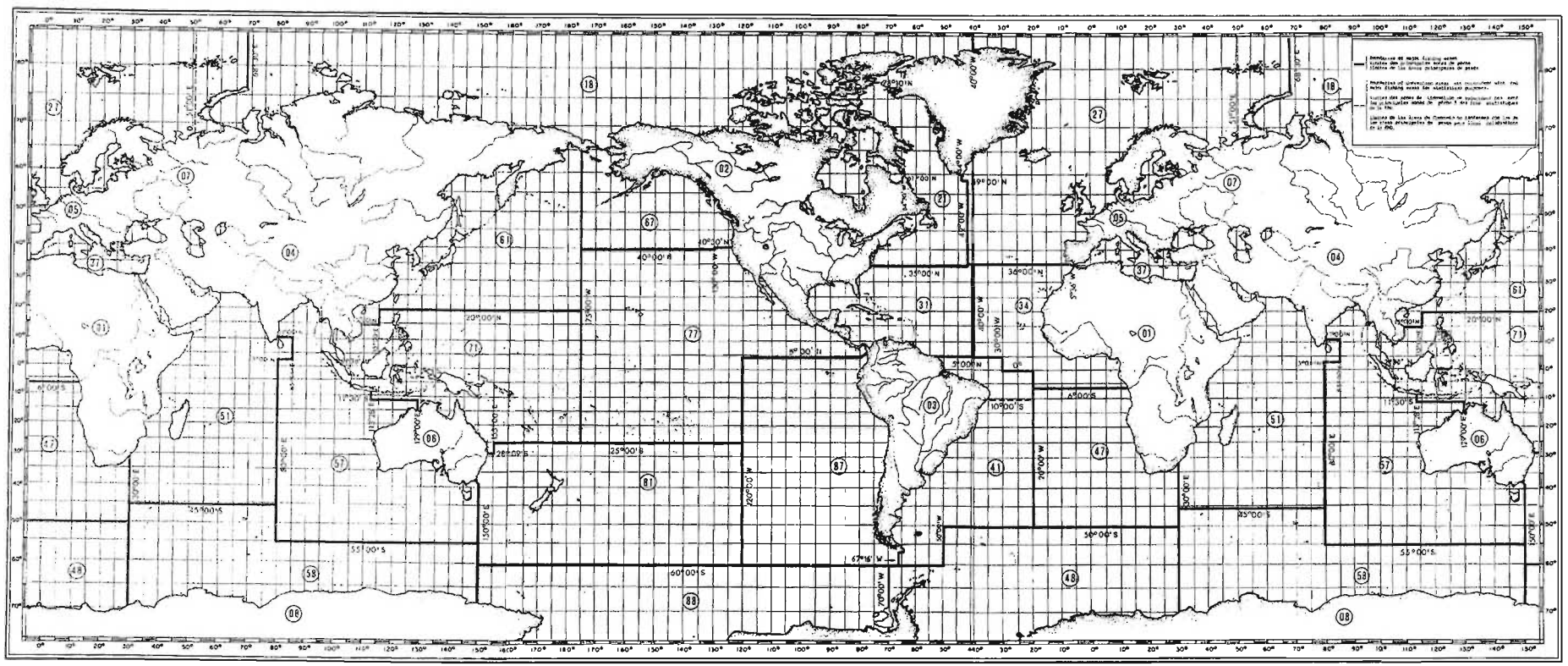


Figure 1.1: Map showing FAO fishing areas (FAO, 1998).

the 22 FAO areas (Figure 1.1) reported catches of serranids. The figures are based on *reported* catches, and hence are underestimates, particularly in the case of artisanal fisheries, for which catches are rarely recorded. Highest catches were reported from the central/western Atlantic, which is probably a reflection of the more rigorous reporting in this area. Catches from the Indian Ocean region would undoubtedly be much larger if these data could be more accurately obtained. Given the uncertainties and disparities in the collection of catch data, the observed overall trend in increased catches of serranids from 1987 to 1996 could be an artefact of better reporting, or advances in fishing technology, rather than greater catches.

Throughout their range, serranids are mainly caught on hook and line (including longlines), but also caught by other fishing gears, such as nets, traps and by spearing. They are predatory fishes, and are often curious or unwary of fishers and fishing gear (Stolzenberg, 1994), which makes them vulnerable to capture. The flavour of their flesh is esteemed and highly valued in fish markets (Table 1.3) and, consequently, serranids are targeted wherever they occur. Their high value has reached extreme proportions in the case of the trade in live reef fishes for food, and some *Epinephelus* species attain prices of over US$100 per kg (Lau and Parry-Jones, 1999). These extremely inflated values contribute to the high levels of directed fishing effort on this family.

Table 1.3: Prices of whole, fresh fish in the United States (December 2000). Prices are converted to US$/kg. The serranid species is indicated in bold. Source: Fish Info Service (http\\:www.fis-net.com\).

Species	Common name	Price US$/kg
Lophius americanus	Monkfish	7.72
Lutjanus campechanus	Red snapper	7.17
Mycteroperca bonaci	**Grouper**	**6.62**
Salmo salar	Salmon	4.08
Coryphaena hippurus	Dorado	3.86
Hippoglossoides platessoides	Plaice	3.53
Merluccius bilinearis	Hake	2.21
Micropogonias undulatus	White croaker	1.76
Peprilus triacanthus	Butterfish	1.65

In South African linefisheries, serranids only occur to any significant extent in catches on the east coast, and particularly in the province of KwaZulu-Natal (Figure 1.2 and Table 1.4). However, they have been identified as priority species from both management and research perspectives (Wallace and van der Elst, 1983; van der Elst and Adkin, 1991; Mann, 2000), and form a substantial part of the linefish catches by both recreational and commercial sectors in this province (Chapter 2).

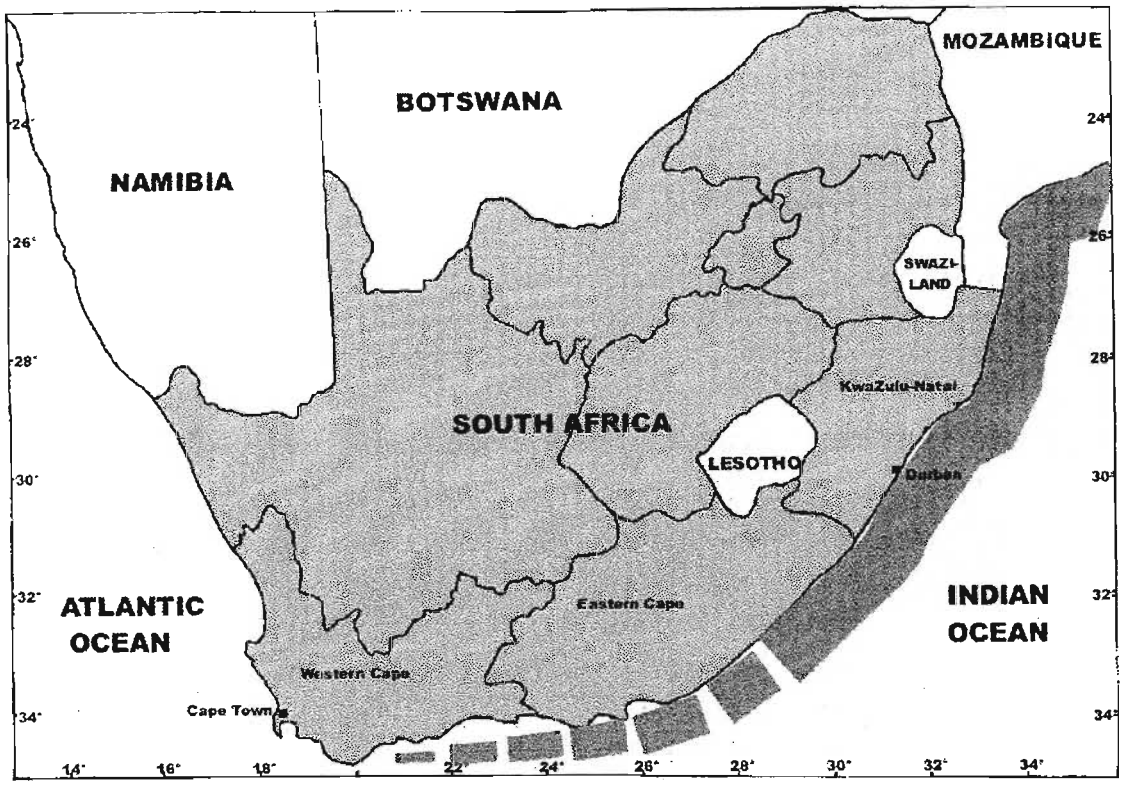


Figure 1.2: Map of southern Africa, showing the province of KwaZulu-Natal, with a dark grey band indicating the main distribution of epinepheline serranids.

Table 1.4: Most important fish families in catches by the South African commercial linefishery, in three coastal provinces.

Province	Family	Source
Western Cape	Gempylidae, Sparidae, Carangidae	Marine and Coastal Management (1997)
Eastern Cape	Sparidae, Sciaenidae, Merlucciidae	Marine and Coastal Management (1997)
KwaZulu-Natal	Sparidae, Sciaenidae, Serranidae	Penney *et al.* (1999)

Linefisheries present unique problems with regard to assessing their status. Standard surplus production models are not suitable for stock assessments of linefishes for several reasons, including a lack of virgin biomass estimates, poor estimates of current biomass and uncertainty as to the proportions of stock available to the fishery (Butterworth *et al.*, 1989). More particularly, the main input variables to surplus production models (i.e. catch, effort and catch per unit of effort) are poor estimators of linefish biomass because of aggregating behaviour, improvements in fishing gear and techniques (and hence catchability) over time, and the multispecies nature of the catches (Huntsman *et al.*, 1983; Bannerot *et al.*, 1987; Buxton, 1992). Stock assessments of linefish species in South Africa have therefore relied on per recruit modelling e.g. Coracinidae (Bennett, 1988), Sparidae (Buxton, 1992; Punt *et al.*, 1993; Chale-Matsau *et al.* (in press), Scombridae (Govender, 1995) and Sciaenidae (Griffiths, 1997a).

Life history parameters are required inputs for the per recruit approach to stock assessment. These parameters are defined as "the significant features of the life cycle through which an organism passes, with particular reference to strategies influencing survival and reproduction" (Lincoln *et al.*, 1982). They have long been identified as being useful to fisheries biologists (Beverton and Holt, 1959; Beverton, 1963), since the life history of a species will determine its response to fishing pressure (Adams, 1980; Garrod and Horwood, 1984; Jennings *et al.*, 1998). In South Africa, initial fisheries management measures for linefish species were based on the life histories of the species concerned, whereby species that were thought to be long-lived, late-maturing and endemic were classified as vulnerable, and hence required more conservative catch limits (van der Elst and Garratt, 1984).

The productivity of a species from a fisheries perspective is thus mediated by life history parameters such as natural mortality rate, growth rate and age at maturity. In terms of classical ecological survival strategies, *r*- and *K*-selected species (Pianka, 1974) can be characterised in terms of their life history parameters (Table 1.5). In general, *r* strategists will maximise reproductive output at the expense of somatic growth, while *K* strategists maximise their growth with a corresponding delay in reproduction. The two strategies can be considered to be at opposite ends of a continuum along which species can be arranged, although this is by no means definitive.

Table 1.5: Life history parameters as predicted for *r*- and *K*-selected fish species [after Adams (1980) and Darwall *et al.* (1992)].

Parameter	*r*-selected	*K*-selected
Maximum size	Small	Large
Growth rate	Fast	Slow
Maximum age	Low	High
Age at first maturity	Low	High
Natural mortality	High	Low

In general, serranids may be classified as *K* strategists, with the characteristic life history parameters listed in Table 1.5. These characteristics are typical of species prone to over-exploitation (Jennings *et al.*, 1998). Indeed, several species of serranids have been reported as being over-exploited (Sadovy and Figuerola, 1989; Huntsman *et al.*, 1994; Sadovy, 1994; Huntsman *et al.*, 1999; Coleman *et al.*, 2000; Wyanski *et al.*, 2000). Serranids also have other characteristics that increase their potential vulnerability to over-fishing. Many species form spawning aggregations which can increase their catchability during particular times of the year (Shapiro *et al.*, 1993a; Sadovy *et al.*, 1994a; Koenig *et al.*, 1996). Also, several species have been shown to be protogynous hermaphrodites i.e. they change sex from female to male (Bouáin and Siau, 1983; Shapiro, 1987; Bruslé-Sicard *et al.*, 1992), a reproductive strategy which may be disrupted by fishing (Smith, 1982; Bannerot, 1984; Buxton, 1990; Vincent and Sadovy, 1998; Coleman *et al.*, 1999).

This thesis aims to investigate the life history styles of serranids from the east coast of South Africa, with specific reference to the relevance of these for stock assessment and the resilience of the species to harvesting. The following chapter will describe the fishery for serranids and the population structure of the four investigated species. Reproductive biology will be covered in Chapter 3, and a description given of the gonadal structure, size at maturity and reproductive seasonality. Considerable attention will be paid to evidence for the determination of hermaphroditism and the contrasting reproductive styles of the species investigated. In Chapter 4, the age, growth and mortalities of these species will be described, particularly the validation of age estimates, comparative lengths at age and the determination of fishing and natural mortality rates. Stock assessments of the four species by means of per recruit analyses will be presented in Chapter 5. The concluding chapter will summarise the findings of the previous chapters and discuss them with reference to fisheries management in South Africa.

CHAPTER 2: DESCRIPTION OF THE FISHERY AND CATCHES

Introduction

It is my intention in this chapter to describe the study area and the fishery for serranids in KwaZulu-Natal, as well as the relevant fisheries regulations. This information will assist in the understanding of the fishery and the sampling procedures employed. The species composition and proportions of the serranid component of catches form part of this description, as does information on the size structure of the catches.

Length data are amongst the most basic types of information required by fisheries scientists. Not only are length data relatively simple and cheap to collect, they provide immediate information on the general status and gear selectivity of the fishery. Combined with information on effort, they can also provide a simple index of stock abundance (Gulland, 1975a). Although age-based techniques are generally more precise (Csirke *et al.*, 1985) and mathematically simpler, results based on analyses of length data can be obtained much more rapidly. Consequently, they are increasingly being used in stock assessment and the evaluation of alternative management strategies (Gulland and Rosenberg, 1992). This is particularly so in tropical fisheries, where, amongst other factors, the large number of species and the frequent lack of infrastructure make the use of age-based methods unattractive (Pauly, 1984). In general, length data can be used for rapid stock assessments, and are particularly useful in obtaining a preliminary estimation of the status of the exploited component of the population.

Data on the size structure caught by the different fishery sectors provides information on the part of the population available to, or targeted by, that sector. This information is potentially useful for fisheries managers, since size limits are commonly used in the management of hook and line fisheries. Furthermore, several of the biological characteristics of a species e.g. diet, maturity, fecundity are directly influenced by its size. The length and sex data collected in this study were used to examine disparities in sex ratios between size classes (Chapter 3), and in the preparation of growth curves and age-length keys (Chapter 4). These, in turn, were used to derive overall mortality rates from age-converted catch curves. Length-weight relationships were used to obtain estimates of weights of individual fish, which were used in the calculation of gonado-somatic indices and size at maturity (Chapter 3). Parameters of the length-weight relationship were also required as inputs to per recruit models (Chapter 5).

Study area

The east coast of South Africa, and particularly the province of KwaZulu-Natal, is characterised by two notable features, namely, the narrow width of the continental shelf, and the proximity to the coast of the powerful, southward-flowing Agulhas current (Lutjeharms and Roberts, 1988; Schumann, 1988; Beckley and van Ballegooyen, 1992; Figure 2.1).

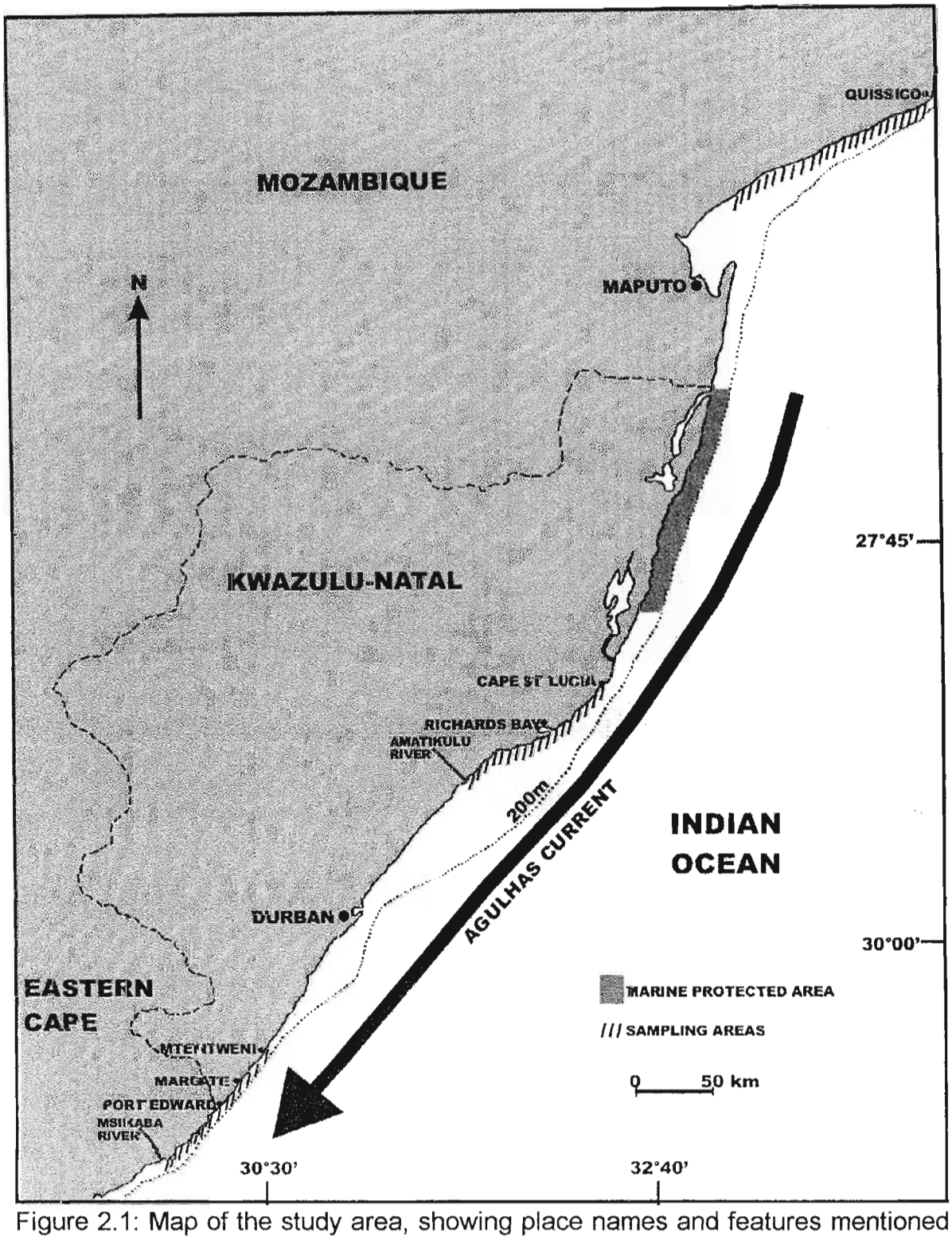


Figure 2.1: Map of the study area, showing place names and features mentioned in the text.

The Agulhas current is fast-flowing, with speeds as high as 2.6 m sec^{-1} being recorded within 10 km of the coast (Shannon, 1989). The shelf waters are current-dominated (Malan and Schumann, 1979; Flemming and Hay, 1988), and the high-energy nature of the coastline results in the water being well-mixed in terms of temperature and salinity (Schumann, 1982). Located south of latitude 27° S, the waters of KwaZulu-Natal are classified as subtropical, experiencing a range of

surface temperatures from 15 to 27°C (Figure 2.2). Limited sub-surface temperature data suggest that the difference between surface and bottom temperature on the shelf (< 100 m water depth) seldom exceeds 5° C (Schumann, 1988; Valentine *et al.*, 1991). Tidal amplitude is about 1.75 m at spring-tide, and the prevailing coastal winds are north-easterly and south-westerly (Hunter, 1988). Winds can attain speeds of over 120 km/h, particularly in the stormy winter and spring months, further contributing to the high energy of the shelf waters.

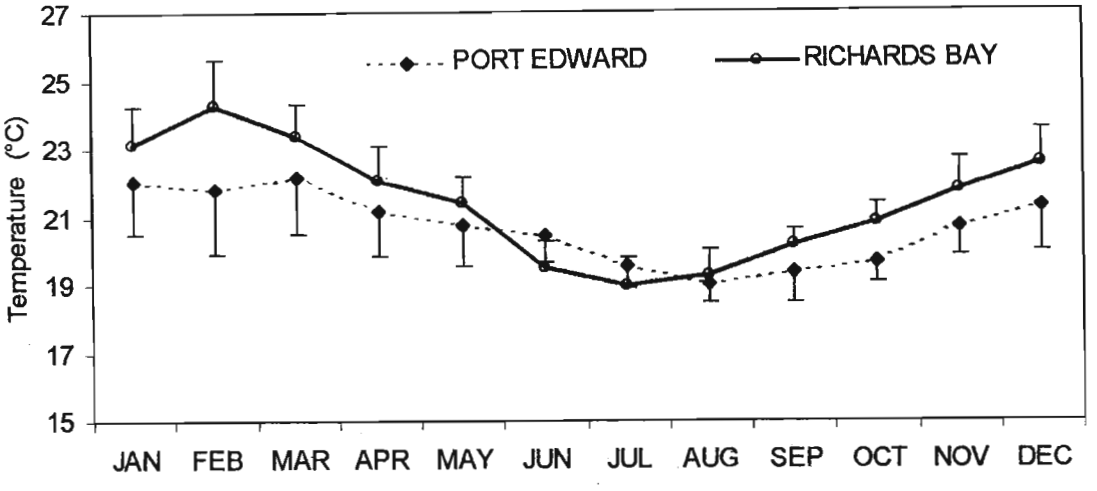


Figure 2.2: Mean monthly sea surface temperatures from the northern (Richards Bay) and southern (Port Edward) KwaZulu-Natal coast, from 1995 to 1997. Monthly data were pooled between years, and the error bars represent one standard deviation. Source: Natal Sharks Board, P/Bag X2, Umhlanga Rocks 4320, South Africa unpubl. data.

The coastline of KwaZulu-Natal is relatively linear, lacking embayments and significant capes. The shelf break is located about 10-15 km offshore in the northern and southern regions, while the central section of the coast is indented, forming a shallow bight (Figure 2.1). The shoreline is comprised of alternating sections of rocky shores and sandy beaches, the latter predominating in the central region. The subtidal rocky substrata with which serranids are associated are situated in shelf or slope waters in depths of up to 270 m. In the northern region of KwaZulu-Natal, these reefs are covered by a veneer of corals, because the water is clearer and warmer relative to the central region of the coast. The reefs in both the latter region and in the south are more temperate in nature, tending to be dominated by algae, ascidians and sponges.

In KwaZulu-Natal, there are two distinct reef strata on which most of the linefishing occurs. The first is a semi-discontinuous line of reefs, formed by ancient, submerged coastal dunes, which closely follow the 50 m isobath. The second zone is located towards the shelf break, and is represented by a rugged profile of pinnacles, drop-offs, narrow shelves and steep slopes in water depths greater than of 100 m (Garratt, 1984). This zone is often strongly influenced by the Agulhas current, and can therefore only be fished in ideal conditions i.e. low wind speeds and slack currents. Apart from these two areas, there are also scattered, low-profile reefs, which are also targeted by fishers.

The sampling ares occur within the province of KwaZulu-Natal, although a small part of the northern region of the Eastern Cape province is also included. Two primary sites were selected as being most likely to produce reasonable samples of serranids, namely the towns of Margate to the south and Richards Bay to the north (Figure 2.1). In close proximity to these towns are several launch sites for commercial fishing boats, that operate in the area between the Msikaba River and Mtentweni in the south, and between the Amatikulu River and Cape St Lucia in the north. These areas are designated as southern and northern sampling regions respectively. For the sake of brevity, the text and figure and table captions will refer to samples collected "from KwaZulu-Natal". In addition, some samples of serranids were obtained on an *ad hoc* basis from commercial catches made in southern Mozambique, hereafter referred to as Mozambique.

Fishing gear and craft

The capture of demersal reef fishes in South Africa is conducted almost entirely by means of hook and line, with a limited amount of spearing. This is unlike in many other countries such as Australia, Tanzania, the Philippines and in the Caribbean, where a variety of other gears are also used, including traps, nets, explosives and ichthyocides (Ruddle, 1996). In terms of participants, the South African reef fishery also differs from that in many other countries, as the artisanal sector is very small, while the commercial and recreational sectors are comparatively large (Sauer *et al.*, 1997a). This can probably be partly ascribed to the rough, exposed nature of the coastal waters, access to which requires robust, engine-powered craft which can withstand these conditions.

In the recreational sector, reef fishes are caught by spearfishing and angling with rod and line from the shore and from boats, while commercial fishers operate exclusively from boats, using handlines or rod and line. The South African boat-based linefishery, particularly on the east coast, is further distinguished from other linefisheries by the type of fishing craft most commonly utilised i.e. the ski-boat. These are small (5-8 m length) craft, constructed of marine ply and/or fibreglass, that are powered by outboard motors. They originated in the province of KwaZulu-Natal during the 1950s, and were specifically designed to be launched through the surf (Garratt, 1984). The craft are transported on trailers drawn by four-wheel drive vehicles, and hence are able to be launched wherever there is access to the sea. Their mobility and ease of launching revolutionised the linefishery in KwaZulu-Natal, because access to fishing grounds was no longer restricted to areas in close proximity to harbours (Penney *et al.*, 1999). Crew numbers average about three for recreationals and six for commercials (Mann *et al.*, 1997). Most of the boats are equipped with echo sounders, Global Positioning Systems and VHF radios. The outboard motors that are used can generate from 50 to 115 HP, and have an effective range of up to 100 km. Fishing trips are mostly restricted to daylight hours and can occur on a daily basis throughout the year. However, because of frequent unsuitable weather conditions, a commercial skiboat will launch an average of 135 times per year in KwaZulu-Natal, while recreational crews launch about 39 times per year (Mann *et al.*, 1997).

The fishing gear used by most commercial skiboat operators in KwaZulu-Natal consists of a stout fibreglass rod and a centre-pin, ungeared reel up to 30 cm in diameter. The monofilament nylon fishing line has a breaking strain of up to 52 kg, and is rigged with a trace of between 5 and 15 hooks. The hooks are attached to monofilament traces 20 - 60 cm in length, which are in turn attached to swivels on the main line. Hook size increases from top to bottom, which is relevant to the targeting of serranids, since the larger individuals of this family are mostly caught on the bottom two hooks (Ritz Louw, commercial fisher, Port Edward, South Africa, pers. comm.). The trace is sent to the sea bed with a steel weight of 0.5 to 1 kg in weight, depending on fishing conditions (wind, currents, depth, etc.). Bait varies according to availability and price, but consists mostly of sardines (*Sardinops sagax*), squid (*Todarodes* spp) and fillets of sub-legal sized individuals of target fish species such as slinger (*Chrysoblephus puniceus*). The gear and bait are similar to that used on recreational skiboats, except that the hooks are fewer in number and the breaking strain of the line is generally lighter. Fishing on reefs is conducted either at anchor, or more commonly, by drifting.

As with most other species in KwaZulu-Natal commercial linefish catches, serranids are generally either gutted at sea or on the beach after a fishing outing. No other processing takes place, and the catch is usually either sold fresh to local dealers or occasionally directly to members of the public. The dealers place the catch on crushed ice, and either sell it to outlets on the coast, such as fish shops, markets, restaurants and hotels, or transport it by vehicle or aircraft for resale to dealers located around the city of Johannesburg some 700 km inland.

Current management of serranids

The South African Living Marine Resources Act of 1998, with its associated regulations, requires all participants in the linefishery (subsistence, commercial and recreational) to possess a fishing permit. Recreational fishers may not sell their catch, and subsistence fishers may only sell catches within their community. Commercial linefishing effort in the province of KwaZulu-Natal is restricted by a limited number of permits (115 full-time commercial skiboat permits) while the recreational and subsistence sectors are open access (unlimited numbers of permits). With regard to serranids, catching of brindle bass (*Epinephelus lanceolatus*) and potato bass (*E. tukula*) has been prohibited since 1992 at the request of the spearfishing community, which was concerned at the low numbers of these fishes and the relative ease with which they could be speared (R. van der Elst, Oceanographic Research Institute, PO Box 10712, Marine Parade 4056, South Africa, pers. comm.). Since 1984, recreational boat fishers have been restricted to a maximum of five specimens of any one or all three of these serranid species: catface rockcod (*E. andersoni*), yellowbelly rockcod (*E. marginatus*) and white-edge rockcod (*E. albomarginatus*). An equivalent bag limit for halfmoon rockcod (*E. rivulatus*) was subsequently introduced in 1992. A minimum size limit of 400 mm (total length TL) for these three species has been applicable to the skiboat sector since 1991, while a 300 mm size limit was applied to *E. andersoni* and *E. marginatus* caught from the shore in Kwazulu-Natal between 1974 and 1998. This suite of regulations had no formal basis, but was based on the limited

biological knowledge available for the species concerned, or based on published information on closely-related species.

Additionally, a large (155 km long, 5.6 km wide) stretch of the northern coast of KwaZulu-Natal is a marine protected area (Figure 2.1). The northern part, the St Lucia marine reserve, was set aside in 1979, and the southern part, the Maputaland marine reserve, in 1986. Serranids, along with all other reef fishes, are protected from harvesting by skiboat fishers and spearfishers within this area. However, of the species that comprise the majority of serranid catches (see below), only *E. rivulatus* has been recorded there in any abundance (Chater *et al.*, 1993; Chater *et al.*, 1995).

Contribution of serranids to linefish catches

Because of its warm-temperate location, KwaZulu-Natal has a diverse marine fish fauna available to the linefishery (van der Elst, 1988). About 120 species of fish are caught by the skiboat fishery, although only 60 of these can be considered important (Penney *et al.*, 1999). In general, the commercial linefish sector in KwaZulu-Natal mostly targets reef fishes, while the recreational skiboat sector targets both pelagic and reef fishes (Penney *et al.*, 1999; Mann *et al.*, 1997).

Since 1985, commercial fishers have been required to submit catch returns to the National Directorate of Marine and Coastal Management that is responsible for the management of marine resources in South Africa. In KwaZulu-Natal, enforcement of marine resource regulations is undertaken by the KwaZulu-Natal Nature Conservation Service (KZNNCS), which also monitors recreational angling catches. Thus, since 1985, KZNNCS officers along the length of the KwaZulu-Natal coast have been obtaining information on recreational shore angling species composition from regular shore patrols. Similarly, these officers collect information on recreational skiboat species composition during catch inspections once the boats have returned to shore. Recreational fishers in the shore angling and skiboat sectors also submit voluntary catch returns. The above data are all submitted to the National Marine Linefish System (NMLS), a national database of information on linefish catches maintained by the National Directorate (Penney *et al.*, 1997). These data were extracted and analysed, and are presented here to illustrate the relative importance of serranids to the South African linefishery. Unfortunately, prior to 1992, a large part of the serranid component of catches was not identified to species level by KZNNCS staff, so the contribution of individual serranids is only presented subsequent to this date.

There has only been one methodical effort to estimate total effort and hence total catch in the various linefishery sectors in South Africa. This survey confirmed that serranids made a notable contribution to linefish catches only along the east coast provinces of South Africa, particularly in KwaZulu-Natal (Sauer *et al.*, 1997b). The survey was conducted in 1995 and, although the values are only based on information for that particular year, they provide the best estimate of total catch available. Using these figures, and the relative proportion of serranids (all species) in the catch, an estimate of an annual catch of about 140 000

individuals or 200 mt of serranids in KwaZulu-Natal can be made for 1995 (Table 2.1). However, owing to the nature of the data collected, there are potentially large biases in this estimate (Mann *et al.*, 1997), and estimates of catches by the recreational sectors in other years have not been made because of the lack of information on total effort.

Table 2.1: Derived estimates of serranid catches in KwaZulu-Natal in 1995, based on estimates of total catches and proportions of serranids in catches by Mann *et al.* (1997).

Sector	Total catch		Proportion of serranids		Estimated serranid catch	
	mt	no. X 1000	% by weight	% by no.	mt	no. X 1000
Shore angling	800	2 400	0.2	0.2	1.8	5
Recreational skiboat	440	240	9.2	9.3	40	22
Commercial skiboat	1 350	1 618	12	6.7	162	108
Spearfishing	100	47	4.8	6.6	5	3

Commercial catch returns of 30 to 75 mt per year since 1985 are equally unreliable, with catches potentially being under-reported by as much as one-third (Sauer *et al.*, 1997a). Historical data are discontinuous, with few data available between 1934 and 1985 owing to non-collection of catch information (Figure 2.3). Although the fishery prior to the 1950s was substantially different, using large, harbour-based vessels as opposed to the current small surf-launched skiboats, it is of interest that historical catches of serranids were much smaller. This is probably because the earlier fishery was mainly targeting a large, aggregating sparid, *Polysteganus undulosus*, catches of which declined drastically in the 1960s (Chale-Matsau *et al.*, in press). Interestingly, the accuracy of the historical data is probably high, since the inspection of a few, large, harbour-based vessels at a single port was much easier than inspecting numerous small boats at many launch sites.

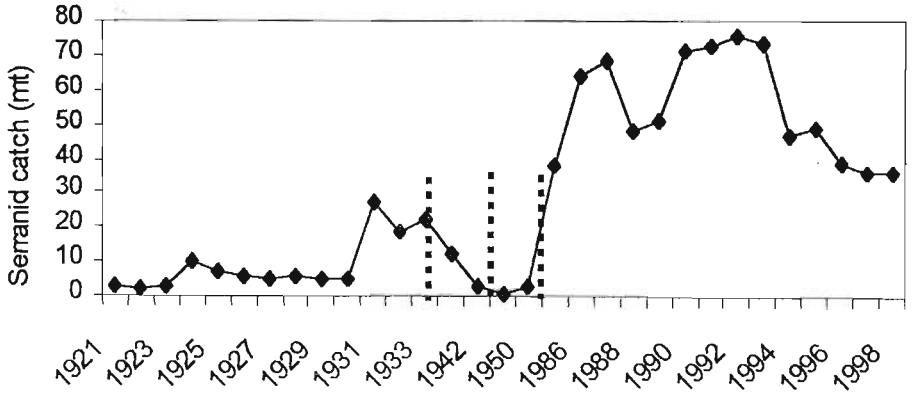


Figure 2.3: Annual catches of serranids by commercial vessels in the KwaZulu-Natal linefishery. Note that the data are discontinuous from 1933-1940, 1943-1950 and 1950-1985 (dashed lines). Sources: Reports of the Natal Fisheries Department (1921-1933); Communication to the Fisheries Development Corporation of South Africa by the Principal Fishing Officer (1940, 1942, 1943); Department of Sea Fisheries, unpubl. data (1950); National Marine Linefish System (1985-1999).

Although total catch and effort are poorly known, the species composition data amassed from KZNNCS inspections and patrols are probably reasonable approximations of actual catches. The overall relative contribution of serranids to catches from each of the four fishing sectors (shore fishing, spearfishing, and recreational and commercial skiboat fishing) in this province is summarised in Figure 2.4. Catches of serranids by shore-fishers are negligible, whereas catches by spearfishers and skiboat fishers comprise roughly 10 percent of the total catch in each of those sectors.

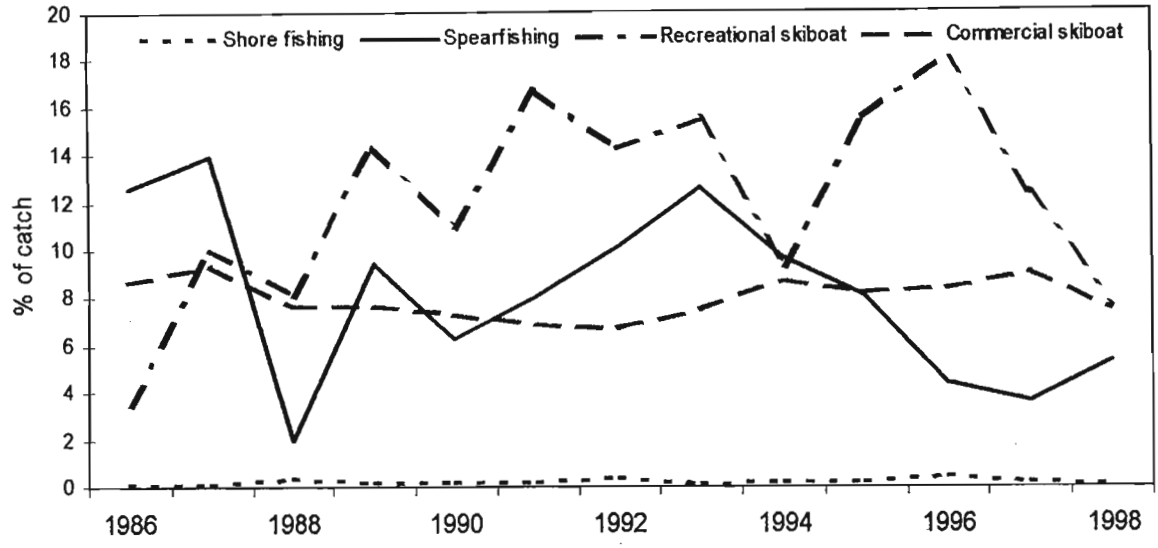


Figure 2.4. Contribution of serranids to overall catches by four fishing sectors on the KwaZulu-Natal coast. Data are percentages of total numbers of fish recorded, except for commercial skiboat catches (percentage by weight). Shore angling data are from KZNNCS shore patrols (n = ~896 000), spearfishing data are from voluntary catch submissions by divers (n = 11 482), recreational skiboat data are from KZNNCS catch inspections (n = 10 672) and commercial skiboat data are from catch submissions (n = 83 204).

Although there are about 45 species of serranids potentially available to fisheries in KwaZulu-Natal (Heemstra and Randall, 1986), only four species regularly occur in skiboat catches, namely *E. andersoni*, *E. marginatus*, *E. albomarginatus* and *E. rivulatus*. Other serranids occasionally observed in catches included tomato rockcod (*Cephalopholis sonnerati*), orange-spotted rockcod (*E. coioides*), dot-dash rockcod (*E. poecilonotus*), yellowtail rockcod (*E. flavocaeruleus*) and moustache rockcod (*E. chabaudi*). Shore angling catches of serranids consist almost exclusively of *E. andersoni* and *E. marginatus*, while spearfishers also harvest these two species as well as orange-spotted rockcod, malabar rockcod (*E. malabaricus*) and greasy rockcod (*E. tauvina*).

I found spatial differences in the skiboat sector in both the overall contribution of serranids to catches and in species composition. Serranids, as a group, made a greater contribution to both commercial and recreational skiboat catches in the north than in the south (Figures 2.5 and 2.6). For example, serranids were absent from only 6 % of commercial catches on the north coast, compared to 38 % on the south coast. In both areas, but particularly in the north, *E. andersoni* dominated

the serranid component of both commercial and recreational catches, whereas in the south, *E. marginatus* and *E. albomarginatus* were of greater importance (Table 2.2).

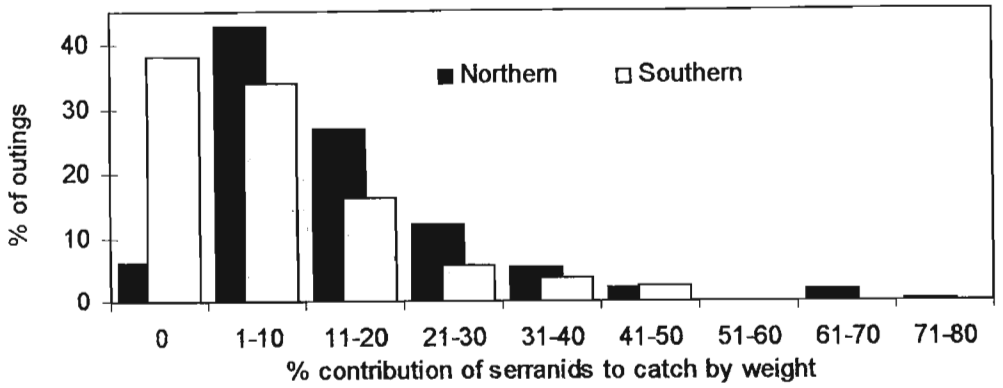


Figure 2.5: Percent contribution of serranids by weight to daily catches by commercial skiboats in KwaZulu-Natal. Data collected by KZNNCS officers during catch inspections (northern n = 227, southern n = 250) from 1995 to 1998. See text for explanation of northern and southern areas.

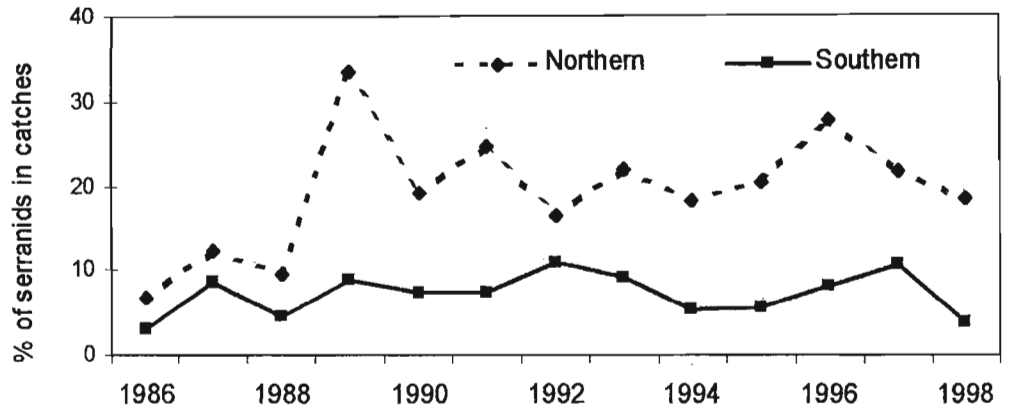


Figure 2.6. Percent contribution of serranids (by number) to daily catches by recreational skiboats in KwaZulu-Natal. Data collected by KZNNCS officers during catch inspections (northern inspections n = 4138, southern n = 3349).

Table 2.2: Overall percentage contribution of four serranid species to the total serranid component of skiboat catches off KwaZulu-Natal. Values are percentages based on the numbers of serranids in catches in which at least one serranid species occurred.

Species	Commercial (n = 123 outings) (Mann *et al.*, 1997), (Fennessy, this study)		Recreational (n = 6 349 outings) (KZNNCS catch inspections, 1992-1997)	
	North	South	North	South
E. andersoni	66.2	37.9	79.7	51.8
E. rivulatus	28.6	25.1	8.7	13.4
E. marginatus	3.5	18.2	6.3	7.1
E. albomarginatus	1.5	18.8	1.1	14.3
Unidentified	-	-	4.2	13

Population structure

Methods

Earlier in this chapter, reference was made to the collection of fishery-dependent data (both recreational and commercial) at two main sampling sites (northern: Richards Bay; southern: Margate) that were selected because they presented the best opportunities for obtaining samples. All individuals of *Epinephelus andersoni*, *E. rivulatus*, *E. marginatus* and *E. albomarginatus* encountered from 1995 to 1997 at Richards Bay and Margate were measured to the nearest mm (total length TL) as part of regular monthly sampling (see Methods in following chapters). Whenever time and logistics permitted, ungutted fishes were weighed to the nearest gram. Additional specimens of sub-legal size (i.e. <400 mm TL) were obtained on an *ad hoc* basis from the Durban area by means of rotenone, spearfishing and linefishing (fisheries-independent collection). To increase the numbers and size range of fishes used in the calculation of length-weight parameters, historical data from serranids collected prior to 1992 as part of a monitoring programme by the Oceanographic Research Institute were also used. Parameters of the length-weight relationship (Wt g = a. (TL mm)^b) were estimated by least-squares linear regression of log-transformed variables.

To examine the size structure of populations exploited by other sectors of the fishery i.e. recreational skiboat, shorefishing and spearfishing, tournament results submitted by these sectors to the NMLS from 1995 to 1997 were collated. In these cases, individual weights of fish were converted to lengths via length-weight equations. Differences in fish lengths between commercial and recreational skiboat sectors and between historical (1985-1987) and recent (1995-1997) commercial lengths were compared using t tests and Kolmogorv-Smirnov tests. Length data collected from the Mozambique linefishery during 1996 and 1997 were compared with lengths from the commercial fishery in northern KwaZulu-Natal from 1995-1997. Comparisons for all species, except *E. rivulatus*, were based on lengths ≥ 400 mm (TL) to prevent the influence of the minimum size limits which were imposed in KwaZulu-Natal in 1991. All samples of *E. rivulatus* were used.

Whenever possible, skiboat fishers were questioned regarding the depth at which they had made their catches in order to test for size-related differences in depth distribution. Linear regressions of the form

Length (TL mm) = m (depth m) + c

were obtained by minimising the sum of squared differences between observed and predicted lengths. The level of significance of the slope of the regression was determined by ANOVA.

Results

The length frequency distributions of the four species of serranids caught in three different sectors of the KwaZulu-Natal fishery are shown in Figure 2.7. With the exception of *E. marginatus*, the recreational skiboat sector catches proportionally more fishes in the larger size classes than the commercial skiboat sector. The size of fishes caught by these two sectors was significantly different in all four species (Table 2.3). The size of fishes caught by the skiboat and shore fishing sectors were not compared statistically, because the shore fishing sector was regulated by a lower minimum size limit (300 mm TL) during the sampling period. Lengths obtained from spearfishing competitions were too few to warrant presenting ($n < 10$ for each of *E. rivulatus*, *E. andersoni* and *E. marginatus,* while *E. albomarginatus* occurs at depths beyond the range of spearfishers). Similarly, participants in the recreational skiboat fishery and shore fishery seldom encounter *E. albomarginatus* or retain *E. rivulatus*, hence length frequencies for these sectors are either poorly represented or not all.

Neither the mean lengths nor the length frequencies of *E. andersoni* were significantly different from the 1980s to the 1990s (Figure 2.8, Table 2.4). For *E. rivulatus*, the mean lengths from the 1990s were significantly larger than those from the 1980s, and the length frequencies were also significantly different (Figure 2.8, Table 2.4). For *E. marginatus* and *E. albomarginatus*, the earlier mean lengths were larger, but only significantly so for *E. albomarginatus*. The length frequencies of *E. marginatus* from these two periods were also significantly different. For *E. marginatus* and *E. albomarginatus*, mean lengths of fish from Mozambique were significantly larger than in KwaZulu-Natal, and the length frequencies from the two regions were also significantly different.

Table 2.3: Measures of central tendency for lengths (TL mm) of four species of serranids by fishery sector, collected from 1995 to 1997 in KwaZulu-Natal. t is the t test statistic for differences between recreational and commercial skiboat sectors. * denotes significance at the $p < 0.001$ level.

	Recreational skiboat	Commercial skiboat	Shore fishing	Recreational skiboat	Commercial skiboat	Shore fishing
		E. andersoni			*E. marginatus*	
Mean	567.6	544.6	484.9	544.3	601.7	426.1
Std.dev.	106.2	95.6	93.5	115.7	150	75.5
Median	580	544	470	530	585	410
Mode	650	530	410	530	610	430
No.	472	956	127	164	256	69
t	3.74*		-	4.17*		
		E. rivulatus			*E. albomarginatus*	
Mean	354.9	319.9	-	555.6	478.3	-
Std.dev.	40.8	38.3	-	97.9	98.3	-
Median	360	317	-	545	461	-
Mode	311	300	-	510	380	-
No.	31	483	-	47	441	-
t	4.92*		-	5.13*		-

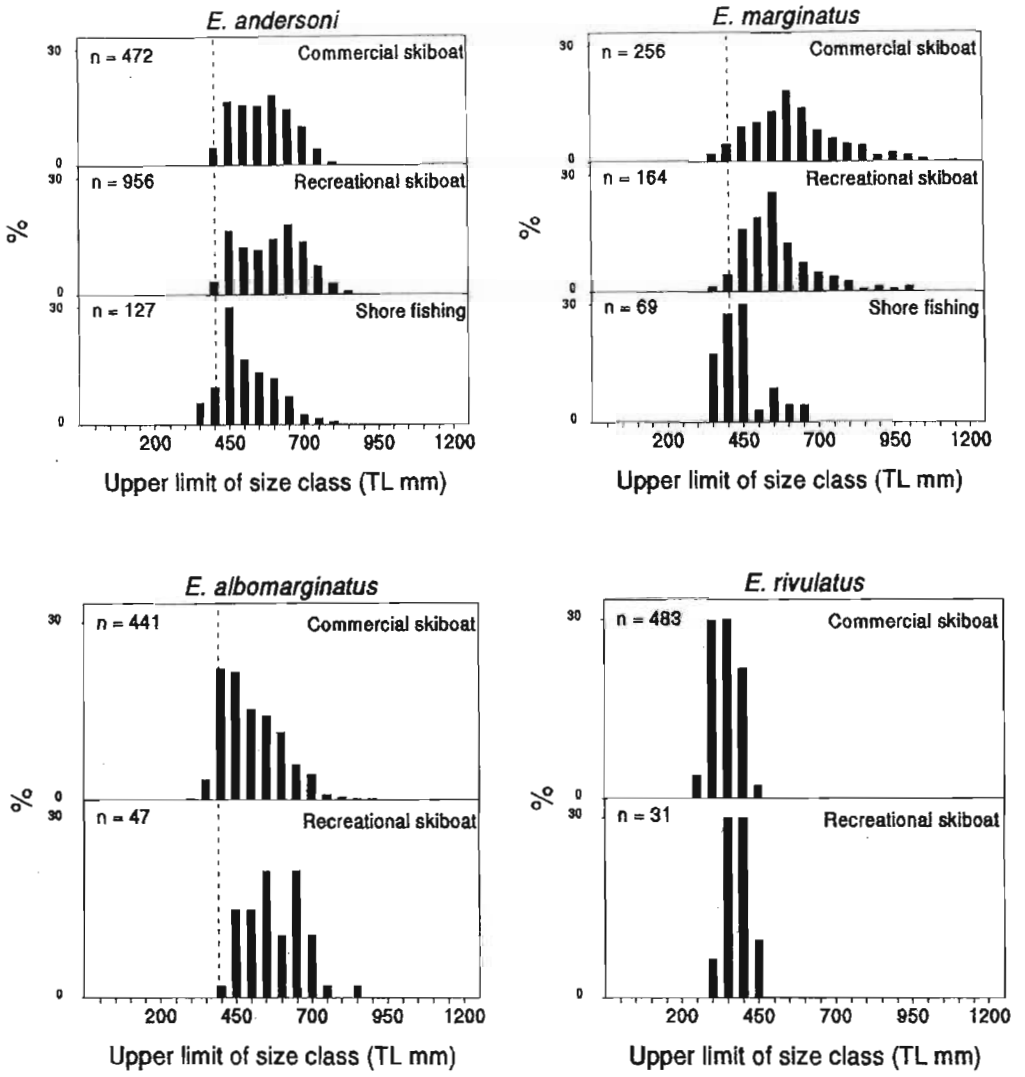


Figure 2.7: Length frequency distributions of four species of serranids collected from 1995 to 1997 in KwaZulu-Natal. The dashed line indicates the minimum legal size limit (400 mm TL).

Table 2.4: Comparative mean lengths (TL mm) and length frequencies of serranids caught by commercial linefishing in northern KwaZulu-Natal (1985-1987 and 1995-1997), and southern Mozambique (1996-1997). Means have been rounded off for convenience; t and D represent test values from the t tests and Kolmogorov-Smirnov tests respectively. Asterisks * and ** represent p values of 0.05 and < 0.001 respectively.

Species	KwaZulu-Natal						Mozambique			
	1985-1987		1995-1997		1980s vs 1990s				KZN vs Moz.	
	Mean	No.	Mean	No.	t	D	Mean	No.	t	D
E. andersoni	551	505	546	512	0.76	0.05*	-	-	-	-
E. rivulatus	288	462	301	214	4.14**	0.14*	-	-	-	-
E. marginatus	660	214	626	101	1.83	0.22*	724	134	5.82**	0.36*
E. albomarginatus	588	129	557	101	2.16*	0.13*	640	313	6.49**	0.35*

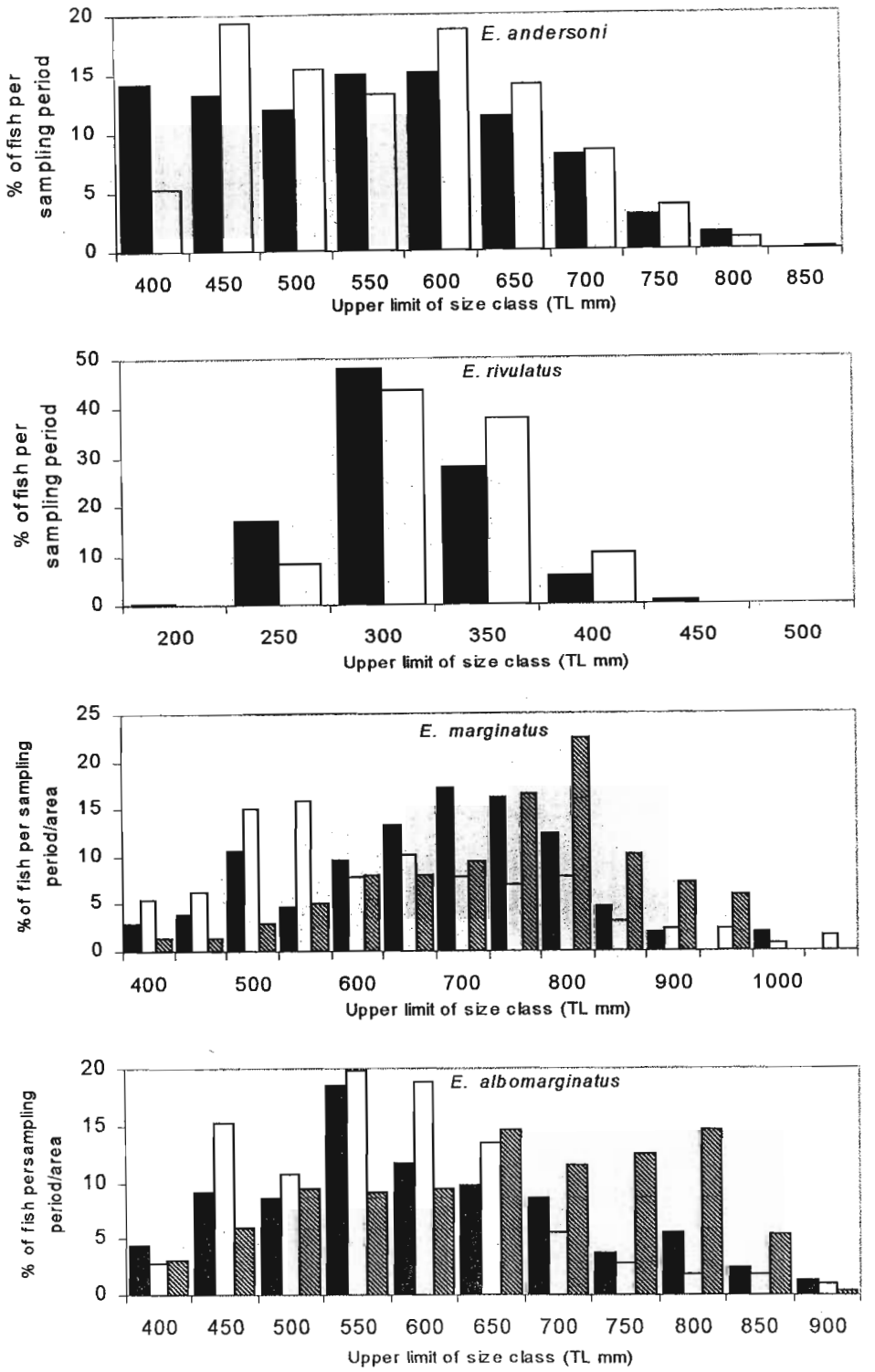


Figure 2.8: Comparative length frequencies of serranids caught by commercial linefishing in KwaZulu-Natal and Mozambique. Solid bars: KwaZulu-Natal, northern sampling area, 1985-1987. Clear bars: KwaZulu-Natal, northern sampling area, 1995-1997. Hatched bars: Mozambique, 1996-1997.

Based on their recorded maximum sizes (Table 2.5), *E. andersoni* and *E. albomarginatus* can be considered medium-sized species, while *E. rivulatus* and *E. marginatus* are small and large-sized species respectively. Based on the

maximum weights recorded by the recreational skiboat sector for the four species, it appears that sampling obtained specimens that were close to the maximum known sizes.

Table 2.5: Maximum lengths and weights recorded for four species of serranids from KwaZulu-Natal from 1985 to 1995. Angling records refers to current maximum weights recorded by the South African Deep Sea Angling Association (i.e. recreational skiboat catch records).

Species	Length (TL mm)	Weight (kg)	Angling records (kg)
E. andersoni	816	6.8	7.5
E. rivulatus	435	1.2	1.6
E. marginatus	1 125	25.1	27.5
E. albomarginatus	870	11.1	12.3

An adequate size range of samples was obtained for the estimation of length-weight parameters (Table 2.6), except in the case of *E. albomarginatus*, small individuals of which proved difficult to obtain. The high r^2 values indicate a good fit to the data. The relatively low value of the *b* parameter for *E. andersoni* is a reflection of the more elongate, slimmer body shape of this species, compared, for example, to the deeper-bodied *E. marginatus*.

Table 2.6: Estimates of length-weight parameters for four species of serranids collected from 1985 to 1997 in KwaZulu-Natal. Standard errors (SE) in brackets; SE for *a* are based on log(*a*).

Species	n	Range TL	*a*	*b*	r^2
E. andersoni	242	110 - 815	$2.26X10^{-5}$ (0.051)	2.905 (0.02)	0.988
E. rivulatus	289	103 - 411	$2.21X10^{-5}$ (0.043)	2.938 (0.03)	0.970
E. marginatus	146	57 - 1125	$1.25X10^{-5}$ (0.055)	3.053 (0.01)	0.998
E. albomarginatus	110	216 - 970	$2.57X10^{-5}$ (0.042)	2.915 (0.03)	0.987

Recreational anglers fished in shallower depths (mean 28 m, SD 16.8) than their commercial counterparts (mean 54 m, SD 21.6). There was a general increase in mean length with depth of capture for *E. andersoni*, *E. marginatus* and *E. albomarginatus*, while *E. rivulatus* showed no such distribution (Table 2.7 and Figure 2.9). The co-efficients of determination (r^2) ranged from low for *E. marginatus* to high for *E. albomarginatus*.

Table 2.7: Parameter estimates (*m*, *c*), co-efficients of determination (r^2) and F values for the linear regression of depth of capture and length for four species of serranids caught by the skiboat fishery from 1995 to 1997 in KwaZulu-Natal. Standard errors in brackets. * denotes significance at the 0.05 level.

Species	*m*	*c*	r^2	F	Residual DF
E. andersoni	2.34 (0.63)	440.1 (35.5)	0.66	13.7*	7
E. rivulatus	-0.67 (0.31)	345.3 (16.6)	0.49	4.76	5
E. marginatus	2.06 (0.75)	493.1 (58.4)	0.43	7.51*	10
E. albomarginatus	2.57 (0.40)	338.7 (32.1)	0.87	41.29*	6

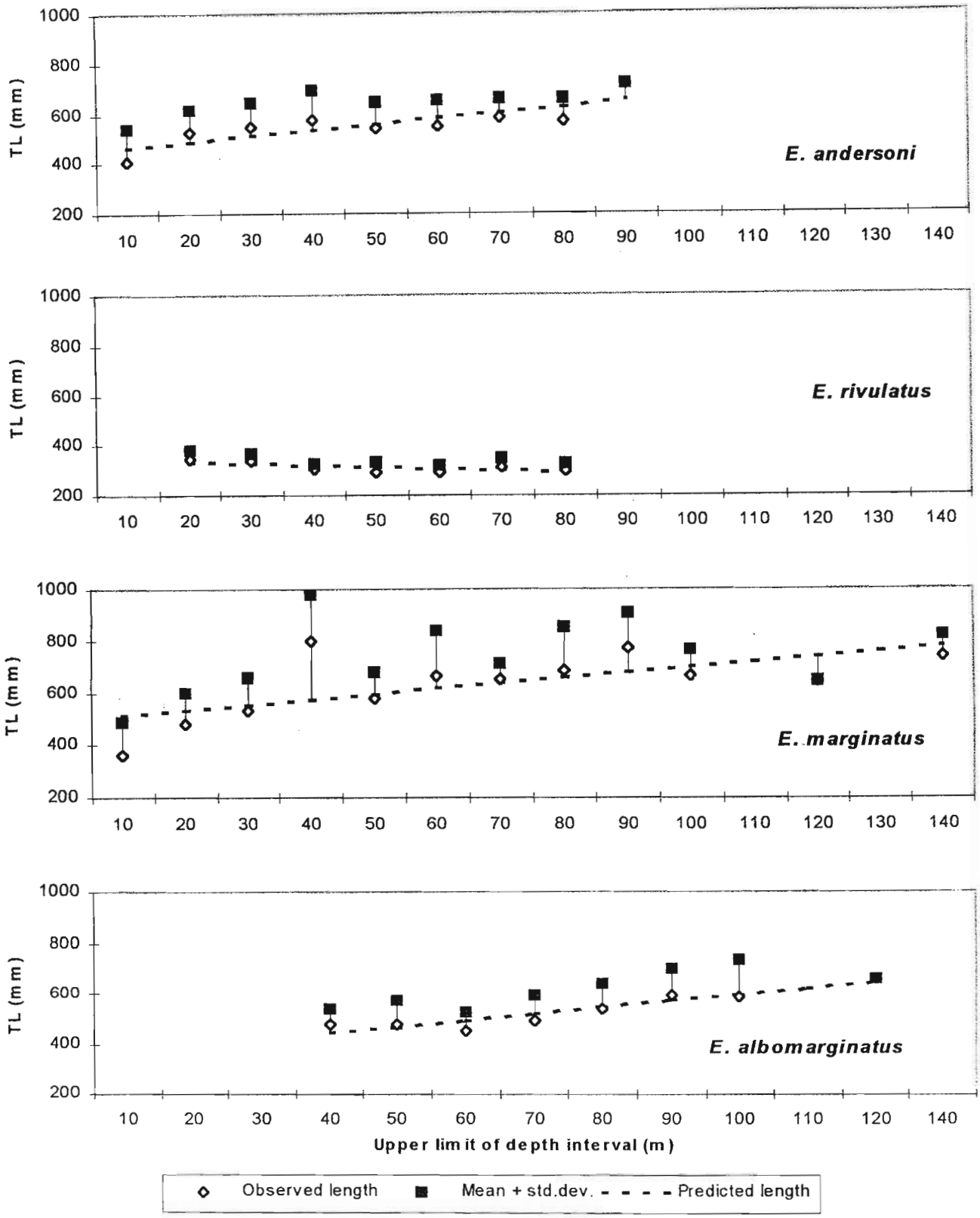


Figure 2.9: Plots of fish length against depth of capture for four species of serranids caught by the skiboat fishery from 1995 to 1997 in KwaZulu-Natal.

Discussion

There is considerable overlap in the size ranges of all four species caught by the recreational and commercial skiboat sectors. However, in the case of *E. andersoni*, *E. rivulatus* and *E. albomarginatus*, the recreational sector tends to catch a relatively greater proportion of fish in the larger size classes. This is perhaps a surprising result, since there is a general increase in mean size with depth and, since recreational anglers fish in shallower depths than their commercial counterparts, one would predict that the former sector would generally catch smaller fish. Despite the fact that many recreational fishers sell their catch, there is less commercial incentive in the recreational sector, as well as targetting of "trophy" fish (Buxton and Clarke, 1989), resulting in the release of smaller (although legal-sized) fishes i.e. high-grading. This argument, though, is countered by the comparatively smaller sizes of *E. marginatus* caught by recreational fishers, which is difficult to explain. Note that the differences in mean sizes of the four species caught by the two sectors, although significant, are not substantial (all <80 mm), so perhaps not too much should be read into the disparity.

Shore anglers tend to catch smaller specimens of *E. andersoni* and *E. marginatus* than skiboat fishers (Figure 2.7, Table 2.3) and, together with the recorded occurrence of small juveniles of these species in tidal pools (Beckley, 1985; Beckley, 2000), provides further evidence for a positive bathymetric gradient in size. Increasing size of serranids with depth has also been reported (Hood and Schlieder, 1992; Brulé and Deniel, 1996). This phenomenon has been reported for numerous species from a range of habitats (Clarke, 1977; Macpherson and Duarte, 1991; Staunton-Smith *et al.*, 1999), although examples of negative gradients (i.e. decreasing size with depth) and uniformity of size regardless of depth are also known (Macpherson and Duarte, 1991). Several reasons for an increase in size with depth have been suggested, ranging from reduced predation and conspecific competition (Helfman, 1978) to potential increases in longevity because of reduced metabolic costs at lower water temperatures (Love, 1970). Whatever the cause, the manifestation of a positive size-depth relationship in serranids on the east coast of South Africa supports the universality of the phenomenon.

Fishing is believed to have caused declines in the mean lengths of a number of reef fish species throughout the world (Jennings and Lock, 1996). The observed evidence in South Africa supports this contention. For instance, there have been declines in the mean lengths and changes in the length frequencies of commercially-caught *E. marginatus* and *E. albomarginatus* over a 10 year period in KwaZulu-Natal. Because the *modus operandi* of the fishery has not changed significantly in KwaZulu-Natal since the 1980s, the observed differences are believed to be a consequence of the sustained high fishing effort and the inability of these species to withstand this pressure. Populations in Mozambique, however, have not experienced a similar decline, even though the methods used in the Mozambican linefishery are essentially the same as those used in KwaZulu-Natal. The difference is that Mozambique populations experienced only light fishing

pressure from 1974 to 1994 (van der Elst *et al.*, 1994) because the country was in a state of war. Consequently, fish stocks reverted to an almost pristine condition (Garratt, 1993). Neither *E. andersoni* nor *E. rivulatus* populations in KwaZulu-Natal experienced reductions in mean lengths over the same period, and possible reasons for this will be discussed in the chapter on stock assessment and in the final chapter.

CHAPTER 3: REPRODUCTIVE BIOLOGY

Introduction

Of all the vertebrates, fishes demonstrate the greatest variety of reproductive patterns, including parthenogenesis, in which reproduction occurs without fertilisation, gonochorism, in which there are separate sexes, and hermaphroditism, in which male and female elements occur together in one gonad (Wootton, 1990). Hermaphroditism has two forms, namely simultaneous, whereby both male and female elements of the gonad mature concurrently, or sequential, in which one element matures first, regresses and is replaced by the other. Replacement of male gonadal elements with female is known as protandry, and the converse is known as protogyny. Additionally, within hermaphrodites, the sex of individuals may be established from a juvenile stage, or be derived by sex reversal. Thus, in diandric protogynous species, males develop both from juveniles and from females, whereas in monandric protogynous species, males are only derived from females (Reinboth, 1967). Although gonochorism is by far the most common sexual pattern in most fish families, hermaphroditism is not unusual, and, when it does occur, it appears to be the dominant sexual pattern within the family (Warner, 1984; Cole and Shapiro, 1990).

Members of the family Serranidae are generally described as being gonochorists or hermaphrodites (either simultaneous or protogynous) (Atz, 1964; Smith, 1965; Chan and Yeung, 1983; Thresher, 1984; Shapiro, 1987). Protogyny appears to be characteristic of the genus *Epinephelus*, because most species examined to date have shown some indication of female to male sex change. Examples include *E. aeneus* (Bruslé and Bruslé, 1975), *E. akaara* (Tanaka *et al.*, 1990), *E. drummondhayi* (Brulé *et al.*, 2000), *E. guttatus* (Smith, 1959; Sadovy *et al.*, 1994b), *E. marginatus* (Bruslé and Bruslé, 1975), *E. morio* (Moe, 1969; Brulé *et al.*, 1999), *E. polyphekadion* (Bruslé-Sicard *et al.*, 1992; Johannes *et al.*, 1999) and *E. tauvina* (Abu-Hakima, 1987). However, not all of these studies provide conclusive proof of protogyny, and one species, *E. striatus* from the Caribbean, has been shown to exhibit gonochorism (Sadovy and Colin, 1995).

In an attempt to standardise the approaches used in diagnosing sexual pattern, Sadovy and Shapiro (1987) produced a critical review of the criteria that could allow a species to be termed hermaphroditic. Diagnostic criteria for protogyny, in order of increasing significance, were a bimodal size and/or age distribution of the sexes, in which males dominated the larger/older classes; a female-biased sex ratio in mature fish; the occurrence in male gonads of a central, membrane-lined cavity which is not used for sperm transport; the occurrence in males of sperm sinuses in the gonad wall; signs of female maturation or previous signs of female functioning such as atretic, vitellogenic oocytes (or post-spawning muscle bundles - Shapiro *et al.*, 1993b) in testes or proliferating spermatogenic tissue in ovaries; and the induction of female to male sex change by using non-hormonal methods. Ideally, all of these criteria should be met, but these authors acknowledge that this is not always possible. The criteria do, however, provide an extremely useful tool in the elucidation of sexual pattern in fishes.

As alluded to in Chapter 1, knowledge of the life history styles of fishes is critical for fisheries management. Of the attributes pertaining to reproduction, size at maturity is of particular importance, since, in combination with other parameters, it has been used to determine the size at which fishes can be harvested. Thus, excessive harvesting below the size at maturity may result in recruitment overfishing, in which case fish do not have an opportunity to spawn before being caught, thereby causing poor recruitment. Differences in size at maturity between males and females may render gear restrictions and minimum legal size limits ineffectual if only one sex is protected by these measures. For instance, if a species changes sex from female to male at a given size, and the size limit is set below that size, then males will not be protected by that management measure. Furthermore, a species that aggregates to spawn over a very short period, or at a restricted locality, may be particularly vulnerable to excessive harvesting once fishers become aware of the aggregation. Hence, the spawning area and the duration of spawning season are also of relevance for management.

The reproductive biology of serranids from southern African waters had not been investigated before this study. In this chapter, I describe the reproductive biology of *E. andersoni*, *E. rivulatus*, *E. marginatus* and *E. albomarginatus*. As initially stated by Reinboth (1970) and re-emphasised by Sadovy and Shapiro (1987), conclusive evidence for protogyny can only be obtained by detailed histological examination, and this approach was used in this study. Particular focus was placed on the elucidation of sexual pattern. Also investigated were the sizes at maturity, and the timing and duration of spawning season for these four species.

Methods

General

The two main sampling sites chosen for this study were Richards Bay in the north and Margate in the south (Figure 2.1), because preliminary sampling revealed that rockcod were regularly caught in these areas. On sampling days, radio contact would be made with boat skippers in either area to establish whether they had caught any of the four species being investigated. If sufficient numbers had been caught to make the trip worthwhile, the skippers were requested not to gut these fish so that I could sample the catch soon after the boats returned to shore. Data collected during sampling were total lengths (mm), gonad weight (to the nearest gram) and, when possible, total ungutted weights, in order to calculate a length-weight relationship. Initial processing of gonads showed that there was no sexual dimorphism, and, unless ovaries were very ripe, that sex of the gonads could not be established macroscopically, so gonads were preserved for histological processing. The majority of samples were collected from catches made by commercial or recreational skiboats, while a few were obtained by shore angling or spearing. Samples were collected on a monthly basis, between May 1995 and September 1997, and attempts were made to obtain 20 gonads per calendar month from both the northern and southern sampling regions.

In addition to the samples collected in KwaZulu-Natal, samples of *E. marginatus* and *E. albomarginatus* were obtained on an irregular basis from commercial catches

made in southern Mozambique. Although the main focus of this study was to investigate serranids in the province of KwaZulu-Natal in South Africa, the fishes from Mozambique were sampled because the fishery had only recently re-opened after a break of about 20 years induced by war. The fish thus formed part of the catch from a virtually pristine fishery (Garratt, 1993). The serranids from Mozambique were part of several consignments of reef fish catches that were imported on an irregular basis. Capture localities for these fishes are only roughly known, but occurred predominantly between Maputo and Quissico (Figure 2.1).

Gonad morphology

The collected gonads remained in 10% formalsaline until processing (usually 6 to 8 weeks post-collection). Initial examination of anterior, medial and posterior sections of 20 gonads from each species revealed that, except for *E. andersoni*, a postero-medial section adequately represented the degree of gonad development. For *E. rivulatus*, *E. marginatus* and *E. albomarginatus*, therefore, a thin (approximately 3 mm) cross-section of each gonad was taken from just posterior to the midsection of the gonad. This procedure was also followed for *E. andersoni*, except that multiple sections were taken of some gonads in order to clarify the development. In particular, this involved the serial sectioning of inactive female and inactive bisexual gonads in order to detect the presence and/or extent of precursive male tissue along the length of the gonad.

The sections were dehydrated in an alcohol series in a Biorad H2500 microwave processor, embedded in paraffin wax, sectioned transversely at 6-7μm, and stained with haemotoxylin and eosin. On examination of the sections, gonads were classified as male, female or bisexual (i.e. containing both spermatogenic and oogenic tissue), and maturity stages were assigned based on the stage of maturation of the tissue.

Spawning season

Length-weight relationships were obtained by fitting a linear curve to log-transformed lengths and weights, using Microsoft Excel. The parameters were used to estimate weights of unweighed fish, which, together with the gonad weights, were used to calculate a gonad index for determination of spawning seasonality in females. For *E. andersoni*, indices were only calculated for fish from the northern sampling region, because there was very little spawning activity in the southern region. For *E. albomarginatus*, indices were only calculated for fish from Mozambique, because there was very little spawning activity in South African waters. A standard gonad index (gonad weight ÷ somatic weight x 100) could not be used for *E. andersoni*, *E. rivulatus* or *E. marginatus*, as analysis of covariance (ANCOVA) showed that the slopes of the regressions of gonad weight against somatic weight were not homogenous between inactive, resting and ripe stages (de Vlaming *et al.*, 1982; Table 3.1). For these three species, the regressions exhibited an exponential relationship, so a log-log transformation of gonad weight and total length was used, which yielded linear relationships with homogenous slopes (Table 3.1). The relative gonad index (RGI) was therefore expressed as a power function of total length:

RGI = (gonad weight/total length ^{X}) x (multiplier)

Where ^{X} is the fitted pooled regression coefficient of log gonad weight against log total length, and the multiplier is simply a scaling factor.

Table 3.1: Results of ANCOVA tests for homogeneity of slopes of regressions of somatic weight against gonad weight, and log total length against log gonad weight. P = 0.05 in all cases. SW = somatic weight (g), GW = gonad weight (g), TL = total length (mm).

	E. andersoni	E. rivulatus	E. marginatus
SW x GW	$F_{(2, 237)} = 24$	$F_{(2, 154)} = 7.7$	$F_{(2, 271)} = 19.4$
Log TL x Log GW	$F_{(2, 237)} = 0.4$	$F_{(2, 154)} = 1.3$	$F_{(2, 271)} = 0.9$
Relative gonad index	$(GW/TL^{4.685})x10^{13}$	$(GW/TL^{4.202})x10^{11}$	$(GW/TL^{6.538})x10^{18}$

Spawning seasonality was also determined by plotting the monthly frequency of each gonad stage in both sexes.

Size at sex change

In protogynous species, the overlap in the range of length frequencies of mature males and females, expressed as a percentage of maximum length, gives an indication of the size range over which sex change can occur. The median value of this range provides an estimate of the size at sex change (Shapiro, 1987). These were estimated, and differences in sizes at maturity from the various sampling regions were tested by a median test based on χ^2 contingency tables (Zar, 1974).

Size at maturity

An estimate of length at 50% maturity for females collected in the spawning season was obtained from a logistic equation of the form:

$y = 1/1(1+\exp(-(x_{mid} - x_{0.5}))/d)$ (Butterworth *et al.*, 1989), where

y = the proportion of mature fish in length class x during spawning season
x_{mid} = the midpoint of the length class
$x_{0.5}$ = size at 50% maturity
d = the width of the maturity ogive.

For the purposes of this calculation, all female fish were classified as mature unless they had been assigned to the inactive or immature gonad stage.

Skipper interviews

To obtain anecdotal information on the likelihood of the four species aggregating for spawning purposes at particular times of the year, commercial skiboat skippers were interviewed during May and June 2000 (Appendix 1). Commercial skippers were chosen because they spend much more time fishing than do recreational skippers, and hence were likely to possess greater knowledge.

Results

General

The majority of samples were collected from boat catches, but samples were not evenly distributed across all calendar months (Table 3.2). Additional specimens were obtained from confiscated, sublegal-sized (<400 mm TL) fish and by spearing of and shore angling for, small specimens of *E. andersoni* (n = 18), *E. rivulatus* (n = 9), *E. marginatus* (n = 12) and *E. albomarginatus* (n = 7). These fishes were mostly obtained from the Durban area, and for purposes of analysis, were combined with samples from the northern sampling area.

Table 3.2: Numbers of gonad samples collected from four species of serranids from May 1995 to September 1997 inclusive. N = northern sampling region (Richards Bay), S = southern sampling region (Margate), M = Mozambican samples. A blank indicates no data.

	E. andersoni		*E. rivulatus*		*E. marginatus*			*E. albomarginatus*		
	Sampling area		Sampling area		Sampling area			Sampling area		
	N	S	N	S	N	S	M	N	S	M
1995										
May		16		8		10	2		1	3
Jun	11		6	9			14		4	7
Jul				12		2			6	4
Aug		22		14	1	27	5		2	10
Sep	9	2	21	2	7	2		4	2	
Oct	16	3	4	6	1	4	9	2	7	30
Nov	53	17	20	4	16	4	3	4	15	11
Dec	54	1	22		4	3	7	15	3	21
1996										
Jan	32	21	25	12	9	5	1	7	20	8
Feb	66	17	23	8	9	4	12		29	8
Mar	37	24	24	6	9	10	24	4	11	11
Apr	48	7	6	13	23	8		6	15	
May	31	16	8	16		9			17	
Jun		39		13	5	41			4	
Jul	8		5	1		6			6	
Aug				1						
Sep	21	10	5	3	3	2			16	
Oct	22	15	19	16	3	25			19	
Nov		15	1	4		5			11	
Dec	5	10		1	13	10			11	
1997										
Jan					6			7		
Feb		4	3	12	6	13		7		
Mar				6		1				
Apr	1		2		3			3		
May			3	3				1		
Jun	4		4		1			2		
Jul	17	19	7		9			16		
Aug	16		7		7			15		
Sep		6		8		2				

Length-weight relationships

Estimates of the parameters of the length-weight relationship are presented below.

Table 3.3: Estimates of the *a* and *b* parameters of the length-weight relationship for four species of serranids. 95% confidence limits are in brackets.

Species	Range (TL mm)	n	a x 10^{-5}	b
E. andersoni	110 – 815	644	1.61 (1.31 - 1.98)	2.95 (2.92 - 2.98)
E. rivulatus	103 – 411	289	2.21 (1.58 - 3.06)	2.94 (2.88 - 3.0)
E. marginatus	57 – 1125	146	1.25 (1.08 - 1.46)	3.05 (3.03 - 3.08)
E. albomarginatus	216 – 970	110	2.57 (1.72 - 3.84)	2.92 (2.85 - 2.98)

Skipper interviews

Seven commercial boat skippers from the northern sampling region were interviewed, with a range of fishing experience from 12 to 28 years. Questioned as to whether they had found that rockcods were particularly common in certain months of the year, skippers did not identify particular species when answering. Some (n = 3) skippers thought that rockcods were more abundant in catches during summer. All felt that the question was difficult to answer, though, and related that several factors, such as the speed and direction of wind and current, influenced catches of rockcod, probably because particular combinations of these environmental conditions allowed them to fish for these species more effectively.

General gonad morphology

In all four species, the gonads were elongate, bilobed organs attached to the wall of the body cavity by mesenteries. The lobes were circular in cross-section and united posteriorly for about 10% of their length. In *E. andersoni*, the right gonad lobe was often longer than the left. Male and female gonads were indistinguishable macroscopically unless in a ripe state. Ripe ovaries were much enlarged with oocytes visible through the gonad wall, and ripe testes produced sperm when pressure was applied. Large, ripe ovaries from *E. marginatus* and *E. albomarginatus* had a lobular appearance. Internally, all gonads had a lumen surrounded by lamellae, apart from an alamellar section approximately opposite the dorsal blood vessel. The assigning of sex and gonad maturity stages to each gonad was based on the most developed stages of germ cell development and their relative proportions within the gonad, following modifications of classifications adopted by Shapiro *et al.* (1993b) and Sadovy and Colin (1995).

Unless otherwise stated, numbers of gonads per gonad maturity stage refer to samples collected in the northern and southern sampling regions only i.e. reference is only made to the Mozambican samples in order to clarify particular aspects of the reproductive biology. All plots were based on pooled data for all years (May 1995 to September 1997) to emphasise seasonal aspects. For convenience, specific features of the reproductive biology of the four species will be discussed immediately following the results section for each species. Thereafter there will be a general discussion in which the reproductive strategies of all four will be contrasted.

Description of gonad stages - E. andersoni

Inactive female (n = 259; Figure 3.1a-c)
This category includes immature fish as well as those fish larger than the size at 50% maturity, and in which there no signs of previous maturity. These gonads contained gonia and closely-packed, previtellogenic oocytes (stages 1 and 2; Figure 3.1a). Several of these fish were larger than the size at 50% maturity in females, and yet were not reproductively active during the spawning season (n = 10; 36 % of all inactive females in the spawning season. This value (36 %) is based on fish from the northern sampling region only, since spawning did not occur in the southern region). It is not known whether inactive fish matured for the first time at a larger size, or whether they had spawned in previous years and then spent one or more reproductively inactive years and regressed to this stage.

Some gonads (n = 56; 22 % of inactive females from both sampling regions) also exhibited a distinctive area of undifferentiated tissue, particularly in the region adjacent to the dorsal blood vessel (Figure 3.1b,c). Fish over a wide range of lengths (366 - 687 mm) exhibited this tissue in varying degrees (Figure 3.1.1). This tissue almost certainly represents presumptive testicular tissue, as determined both by its location as well as by the configuration of the tissue when compared to similar tissue in inactive bisexual fish, in which cysts of spermatocytes are visible. Multiple sections were taken of 20 inactive female gonads that did not exhibit this tissue, from a wide size range of fish, to ensure that small areas of the tissue had not been overlooked. Multiple sections were taken throughout the length of 12 gonads that exhibited this tissue, to determine the extent thereof. These sections showed that, in inactive females, the tissue extended from the junction of the gonadal lobes to the mid-region of the gonad. In cross-section, this tissue occurred on the periphery of the gonad, either in small patches on either side of the dorsal blood vessel, or extending around the circumference of the gonad to varying degrees. Serial sectioning verified that the single postero-medial sections used for most gonads adequately reflected the maximum extent of this tissue in an individual gonad.

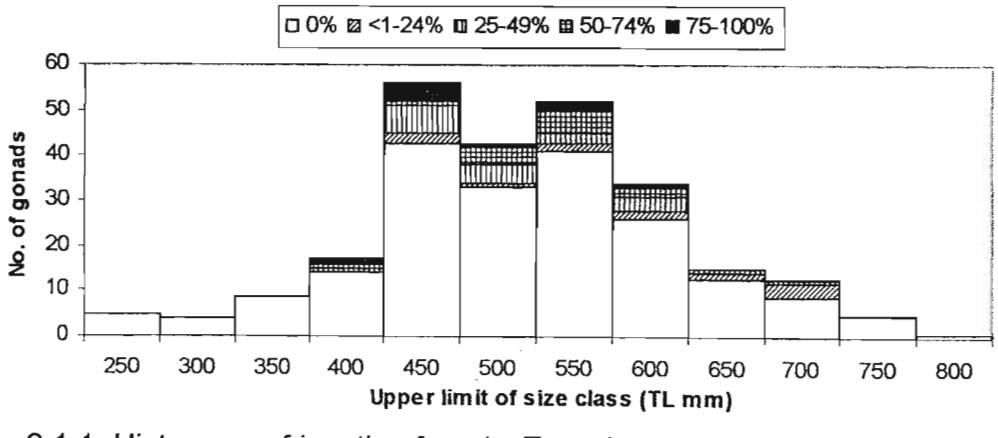


Figure 3.1.1: Histogram of inactive female *E. andersoni*, with relative percentages of presumptive male tissue, determined from complete gonad sections (northern and southern sampling areas; n=183). Percentages are the extent of the presumptive tissue: 0%: no presumptive tissue; 1-24%: extends around 1-24% of the periphery of the gonad (excluding the alamellar region); 25-49%: extends around 25-49% of the periphery of the gonad; 50-75%: extends around 50-75% of the periphery of the gonad; 75-100%: extends around 75-100% of the periphery of the gonad.

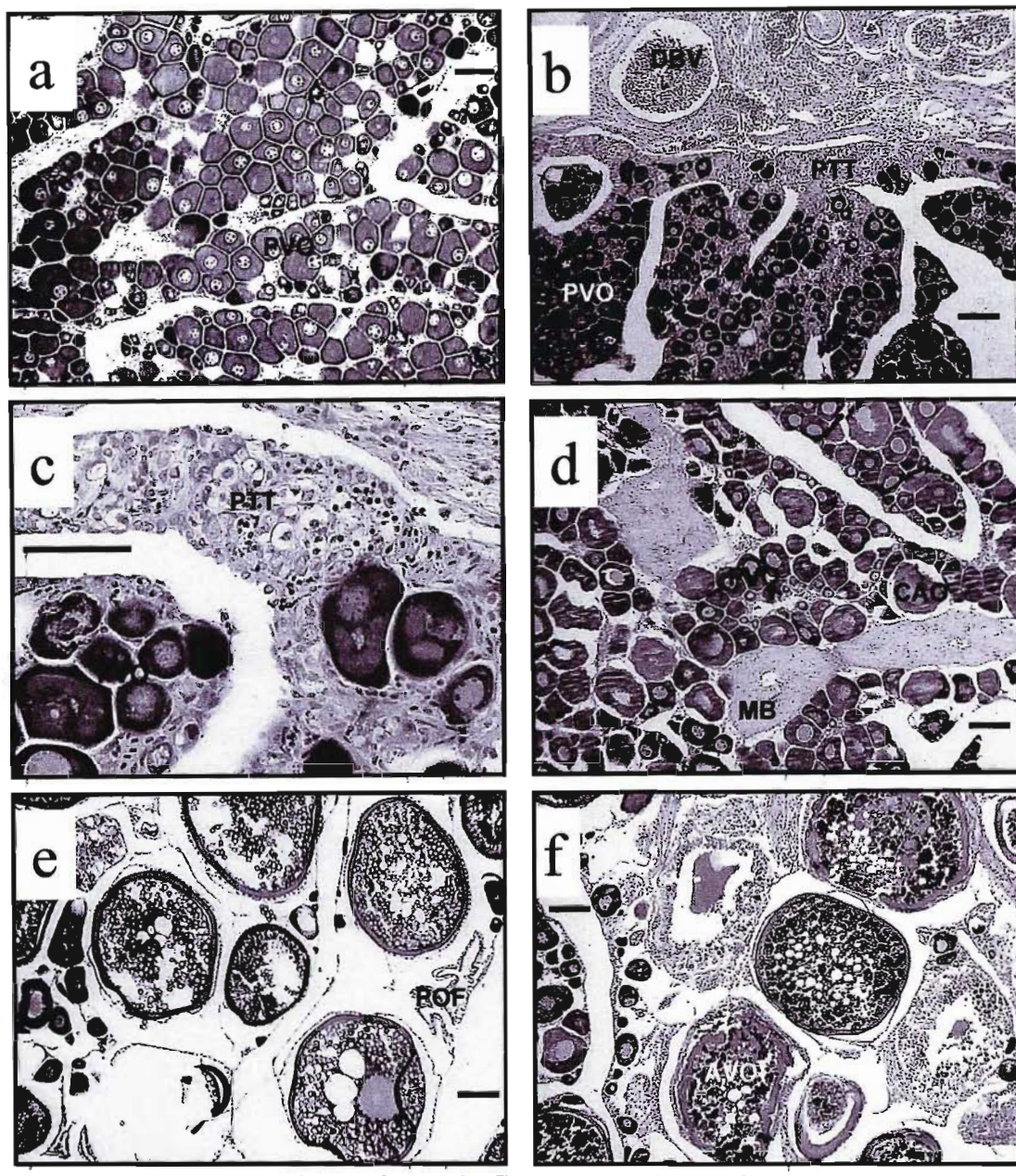


Figure 3.1 Cross-sections of female *E. andersoni* gonads.

a Inactive female gonad showing previtellogenic oocytes (PVO). TL 420 mm, March 1995. Scale bar = 100μ.

b Inactive female gonad, in the region of the dorsal blood vessel (DBV), with presumptive testicular tissue (PTT) and previtellogenic oocytes (PVO). TL 450 mm, March 1995. Scale bar = 100μ.

c Magnified view of (b), showing presumptive testicular tissue consisting of gonial cells. Scale bar = 50μ.

d Mature, resting female gonad, with muscle bundles (MB) and cortical alveolar oocytes (CAO). TL 690 mm, June 1995. Scale bar = 100μ.

e Ripe female gonad, with vitellogenic oocytes (VO) and post-ovulatory follicles (POF). TL 583 mm, November 1995. Scale bar = 100μ.

f Post-spawning female gonad, with atretic, vitellogenic oocytes (AVO). TL 417 mm, January 1995. Scale bar = 100μ.

Mature, resting female (n = 58; Figure 3.1d)
Previtellogenic and cortical alveolar (stage 3) oocytes were present. Very few (n = 8) gonads of this stage were found in the southern sampling region. Some resting gonads exhibited signs of prior ripening i.e. occasional degenerating vitellogenic (stage 4) oocytes, and/or prominent muscle bundles that frequently surround blood vessels. Of the 28 gonads that exhibited obvious muscle bundles, most (26) occurred in fish sampled after the spawning season i.e. in February to May (Figure 3.1.2), hence this feature was used to indicate previous spawning as a female (Shapiro *et al.*, 1993b). Small brown bodies (melano-macrophages) occasionally occurred, but, as these are not necessarily associated with spawning, they were not used as a criterion for assuming prior reproductive activity in females. Several individuals had both muscle bundles and a few scattered cysts (<5) of spermatogenic tissue (stage 1 or 2 spermatocytes) near the dorsal blood vessel.

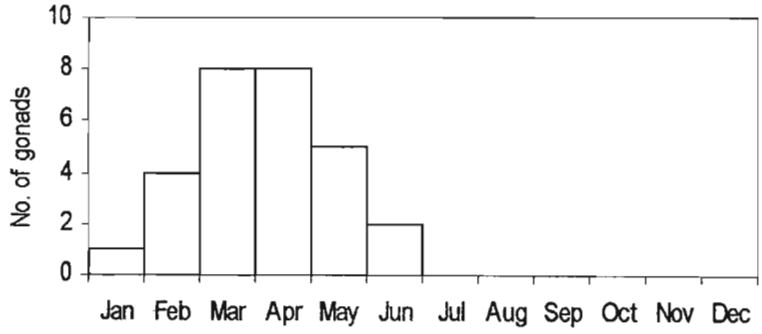


Figure 3.1.2: Monthly occurrence of mature, resting, female *E. andersoni* gonads with muscle bundles. Northern sampling region only; data from May 1995 to September 1997 were pooled.

Mature, ripe female (n = 44; Figure 3.1e)
Gonads were substantially larger than those in a resting stage, and contained previtellogenic and cortical alveolar oocytes, as well as many vitellogenic oocytes. During the spawning season, both hydrated eggs and the occasional post-ovulatory follicle were observed. No ripe female gonads occurred in fish from the southern sampling region, although only one fish larger than the size at 50% maturity was sampled during the spawning season in this region.

Post-spawning female (n = 6; Figure 3.1f)
These gonads showed widespread atresia of vitellogenic oocytes and usually had a disrupted appearance with intralamellar debris and cytoplasmic strands. Previtellogenic oocytes were present. Only 6 gonads in this stage were observed in fish from the northern sampling region, and none from the south.

Inactive bisexual (n = 188; Figure 3.2a-f)
These gonads consisted mostly of previtellogenic oocytes, with a clearly distinguishable area of immature spermatogenic tissue in the area of the dorsal blood vessel (Figure 3.2a,c,d). This area typically consisted of gonia and cysts of early spermatogenic development (spermatocyte stages 1 and 2), and could be quite extensive. Sperm sinuses (splits in the gonad wall) were present in some of these gonads (Figure 3.2b,f). Fish of this stage ranged in size from 370 to 735 mm in length, and there did not appear to be an obvious relationship between fish size and amount of tissue (Figure 3.2.1).

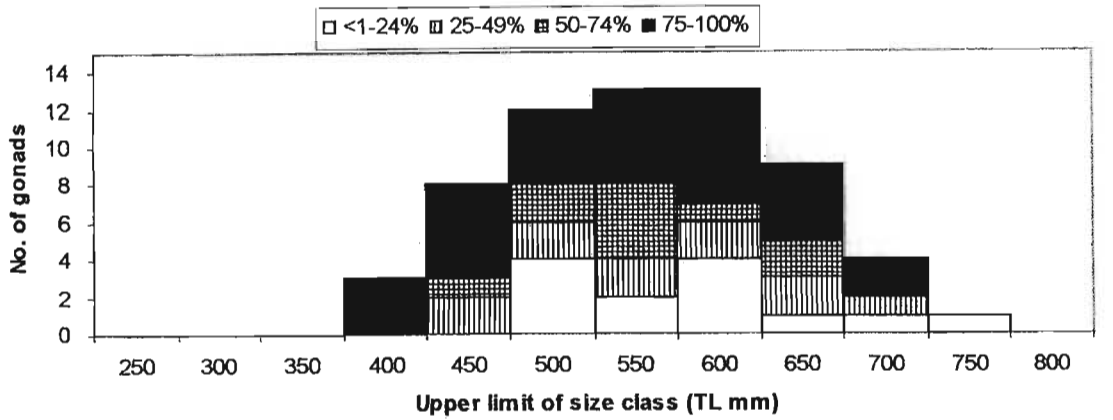


Figure 3.2.1: Histogram of inactive bisexual *E. andersoni* with relative percentages of early spermatogenic tissue, determined from complete gonad sections (northern sampling area only; n = 63). Percentages refer to the extent of the tissue: 1-24%: the tissue extends around 1-24% of the periphery of the gonad (excluding the alamellar region), 25-49%: extends around 25-49% of the periphery of the gonad; 50-75%: extends around 50-75% of the periphery of the gonad; 75-100%: extends around 75-100% of the periphery of the gonad.

Serial sections were made of 10 gonads with varying amounts of this tissue to determine its extent. In gonads in which the initial medial section showed only small, localised areas of gonia and cysts, this tissue was confined to the posterior two-thirds of the gonad, and it was closely associated with the dorsal blood vessel. In gonads with more extensive areas of spermatogenic tissue, the cysts and gonia extended throughout the length of the gonad, and were still mainly parietal in location (Figure 3.2e), although the spermatogenic tissue had started expanding centripetally in the area of the dorsal blood vessel (Figure 3.2f). A clear sequence of development could be followed through the stages of maturation of male tissue, as this tissue proliferated and extended around the circumference of the gonad and also infiltrated the lamellae proximal to the dorsal blood vessel. In this way, the previtellogenic oocytes are replaced and the gonad develops into a functional testis. The male and female elements are not physically separated and spermatogenic cysts also start to arise within the lamellae among the previtellogenic oocytes. Many of these fish (65 % in the northern sampling region, 79 % in the south) were larger than the size at 50% maturity, and a substantial proportion of these (43 % and 41% in these regions, respectively) were inactive even during the spawning season.

Transitional (n = 9; Figure 3.3a,b)
These gonads contained both mature or maturing female (up to early stage 4 oocytes, late stage 3 and cortical alveolus stage) and maturing male tissue at various stages of development, including spermatids and/or sperm. These gonads were distinguished from bisexual gonads by the presence of mature or maturing male and female tissue. The male tissue occupied between one to two thirds of the gonad section, and several gonads contained sperm in the sinuses. Degeneration of at least some of the advanced oocytes was typical, indicating previous spawning activity, or at least progression along the path of maturation as a female. One gonad had muscle bundles as well as sperm in the sinus. These features indicate prior female function and development to a functional male. Gonads in the process of changing sex were recorded in January and April and from June to October.

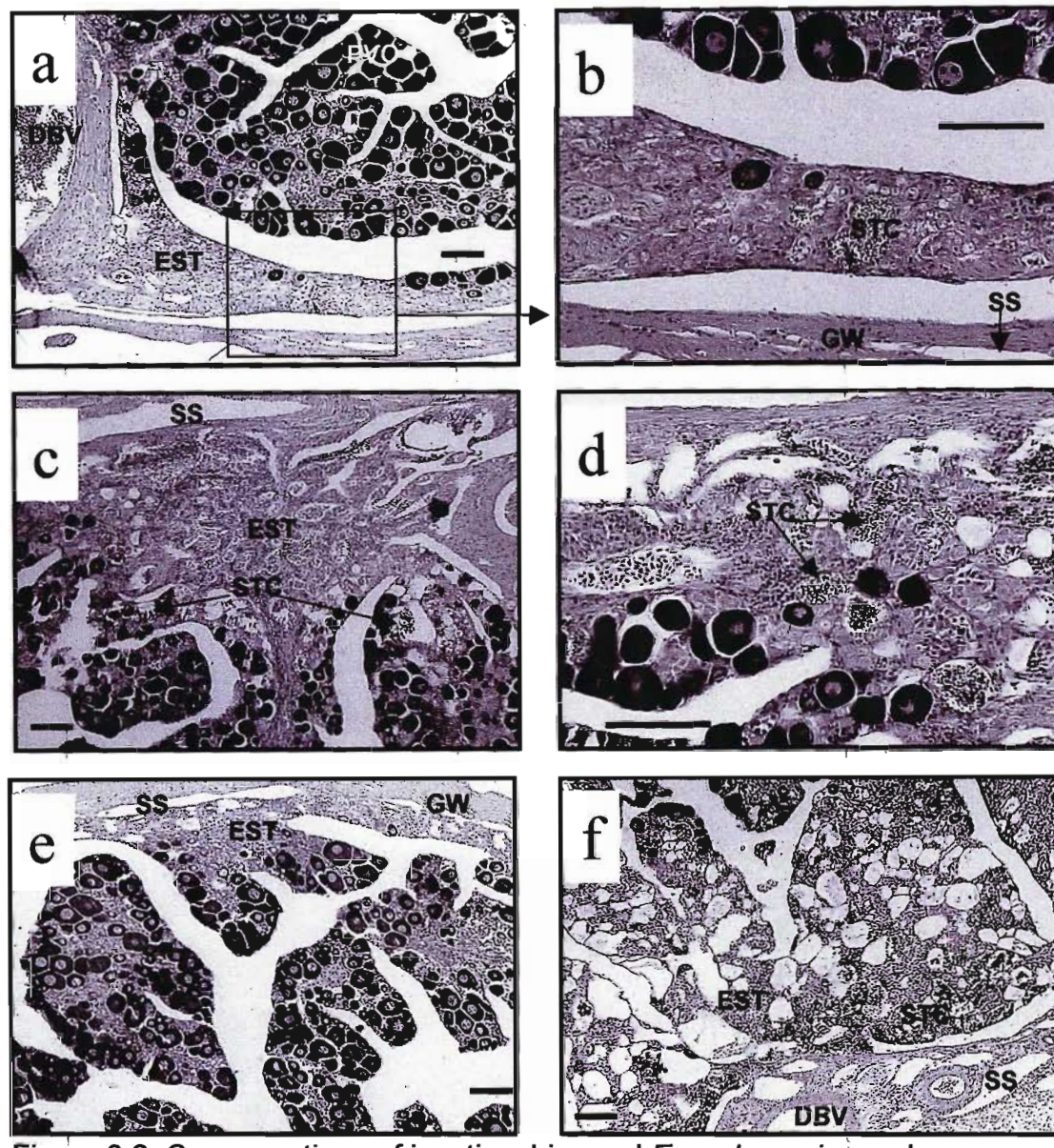


Figure 3.2: Cross-sections of inactive, bisexual *E. andersoni* gonads.

a Section of gonad adjacent to the dorsal blood vessel (DBV), with previtellogenic oocytes (PVO) and early spermatogenic tissue (EST) consisting of gonia and spermatocytes. TL 583 mm, December 1995. Scale bar = 100μ.

b Magnified view of (a), showing cysts of spermatogenic tissue (STC), a sperm sinus (SS) and part of the gonad wall (GW).Scale bar = 100μ.

c Section of gonad adjacent to the dorsal blood vessel, with a more expanded region of early spermatogenic tissue (EST) and cysts of spermatocytes (STC). TL 525 mm, November 1995. Scale bar = 100μ.

d Magnified view of (c), showing spermatogenic cysts (STC). Scale bar = 100μ.

e Section of gonad showing the parietal expansion of the early spermatogenic tissue (EST) proximal to the gonad wall (GW) and a sperm sinus (SS). TL 524 mm, September 1995. Scale bar = 100μ.

f Section of gonad adjacent to the dorsal blood vessel (DBV), with an extensive region of early spermatogenic tissue (EST), cysts of spermatocytes (STC) and sperm sinuses (SS). TL 678 mm, June 1995. Scale bar = 100μ.

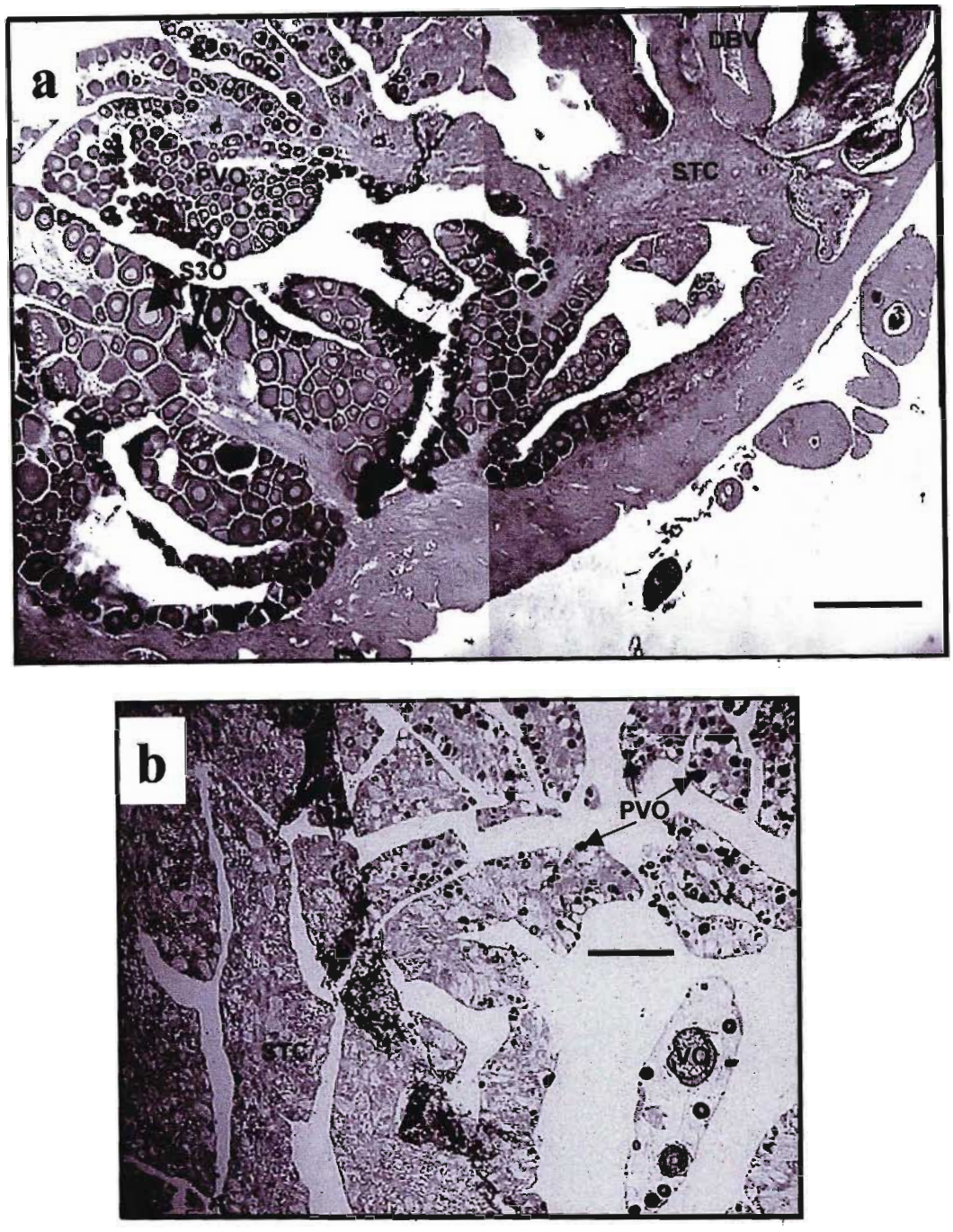


Figure 3.3: Cross-sections of transitional *E. andersoni* gonads.

a Section of a transitional gonad, close to the dorsal blood vessel (DBV), showing cysts of spermatocytes (STC), sperm in the sperm sinus (SSS), previtellogenic oocytes (PVO) and stage 3 oocytes (S3O). TL 622 mm, January 1996. Scale bar = 300μ.

b Section of another transitional gonad showing previtellogenic oocytes, spermatocytes and a vitellogenic oocyte (VO). TL 655 mm, August 1995. Scale bar = 300μ.

Immature male (n = 16; Figure 3.4a)
These gonads were small, compact, and consisted mostly of seminiferous tubules and cysts of gonia, sometimes with occasional scattered patches of stages 1 and 2 spermatocytes. The male tissue was distributed throughout the gonad, unlike in inactive bisexual gonads in which the male tissue was largely restricted to the periphery of the gonad. Stage 1 and 2 oocytes were found in most (n = 14) of these gonads. The oocytes were generally few in number and appeared to be atretic. No sperm (spermatids or spermatozoa) occurred, and sperm sinuses were present in some gonads.

Mature, resting male (n = 63; Figure 3.4b)
Most of the gonad consisted of stage 1 and 2 spermatocytes, with occasional cysts of sperm. In some, small amounts of sperm were also scattered within the sperm sinuses or loosely within lobules. Stage 1 and 2 oocytes were often present and were occasionally numerous. Unlike in some of the mature, resting female gonads, muscle bundles did not occur in resting male gonads. Very few (n = 6) gonads of this stage were found in the southern sampling region.

Mature, ripe male (n = 41; Figure 3.4c)
Stage 1 and 2 spermatocytes were present, but the gonads were dominated by later stages of spermatogenesis. Sperm were present in both the lobules and the sperm sinuses. In some gonads, the lobule walls had split and large areas of amalgamated sperm were evident. Sperm were never observed in the gonadal lumen. No ripe males were found in the southern sampling region, although no males were sampled during the spawning season in this region.

Post-spawning male (n = 31; Figure 3.4d)
These gonads consisted mostly or entirely of seminiferous tubules, sometimes with a few cysts of spermatocytes, and varying amounts of sperm still contained in the sinuses. The gonads often had thick, muscular walls, and the tissue was often disrupted with large empty spaces. Most gonads of this stage were collected from the northern sampling region (n = 30), with only one from the southern region.

Length frequencies and sex ratios

Length frequency histograms of the various sex and maturity stages (Figure 3.5) confirmed that mature fish were far less common in the southern sampling region. Inactive fish were the most commonly sampled fish in both sampling areas, and inactive females and inactive bisexuals, in particular, covered a wide size range. The smallest size classes consisted of inactive females, and mature male sizes overlapped completely with those of mature females.

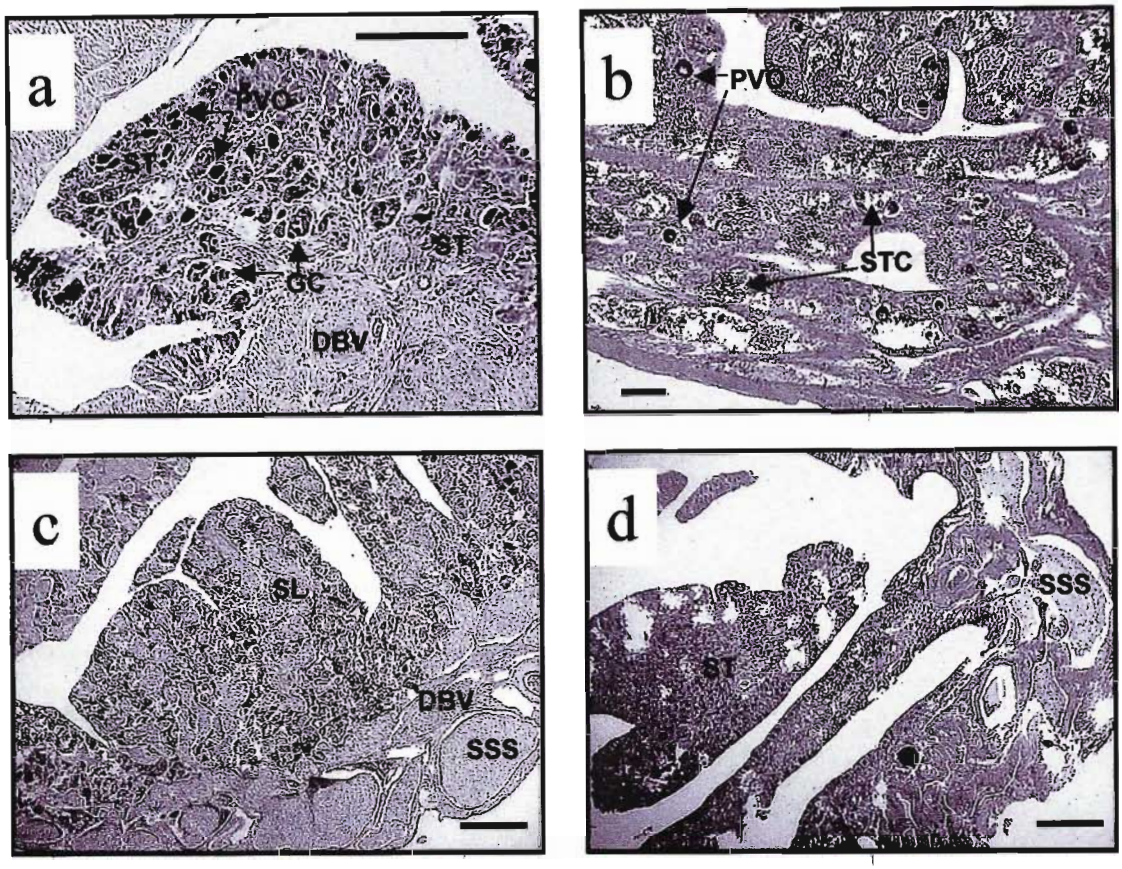


Figure 3.4: Cross-sections of male *E. andersoni* gonads.

a Section of an immature, male gonad, near the dorsal blood vessel (DBV), showing previtellogenic oocytes (PVO), seminiferous tubules (ST) and cysts of gonia (GC). TL 320 mm, February 1996. Scale bar = 100μ.

b Section of a mature, resting, male gonad, showing previtellogenic oocytes and cysts of spermatocytes (STC). TL 669 mm, October 1995. Scale bar = 100μ.

c Section of a ripe, male gonad, near the dorsal blood vessel, showing sperm in the lobules (SL) and in the sperm sinus (SSS). Tl 575 mm, January 1995. Scale bar = 300μ.

d Section of a post-spawning, male gonad, showing seminiferous tubules (ST) and sperm in the sperm sinus (SSS). TL 720 mm, April 1996. Scale bar = 300μ.

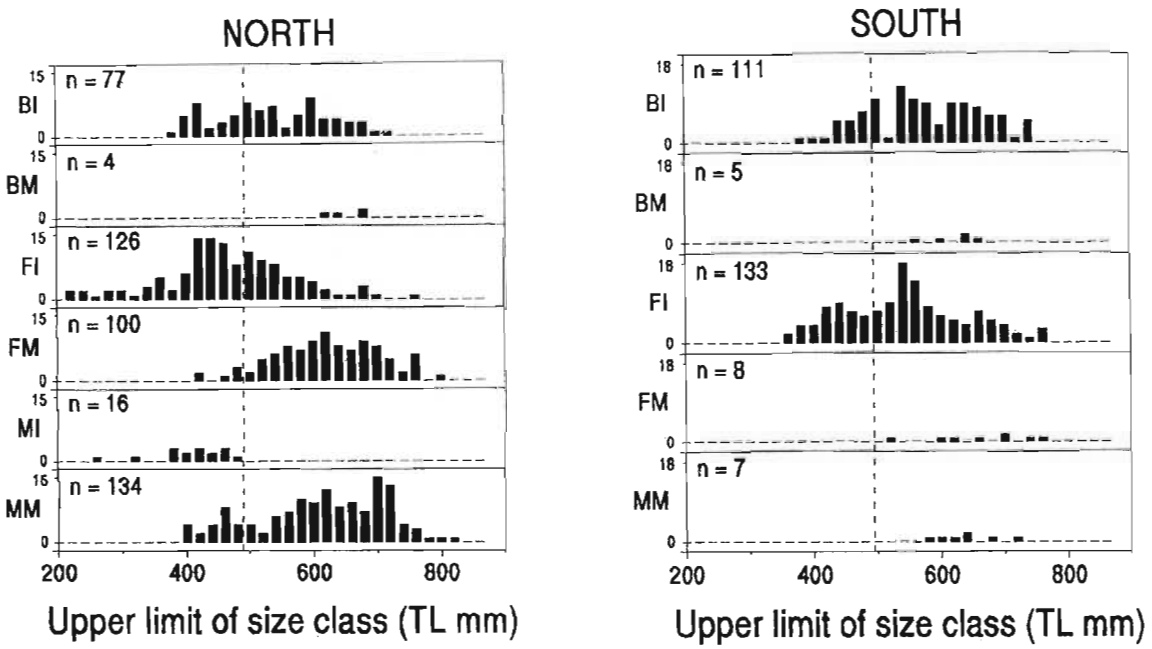


Figure 3.5: Length frequencies (by number) of *E. andersoni* from northern and southern sampling sites. BI = inactive bisexual, BM = transitional (bisexual mature), FI = inactive female, FM = mature female, MI = immature male, MM = mature male. The dashed vertical line signifies length at 50% maturity in females.

Because very little reproductive activity occurred in the southern sampling region, comparisons of lengths and sex ratios of mature fish were based on the northern region only. Mature males ranged in length from 383 mm to 816 mm, females from 417 mm to 783 mm, and their mean lengths [603 mm (SD 100) and 614 mm (SD 80), respectively] were not significantly different ($t = 0.4$, $DF = 232$, $p = 0.05$). Mature males significantly outnumbered mature females (1.34 : 1, $n = 234$, $\chi^2 = 4.94$, $p = 0.05$).

Spawning season

Peaks in gonad indices indicated that the spawning season was extended, from September to January (Figure 3.6) i.e. spring and summer. The relative amounts of each gonad stage on a monthly basis and the appearance of post-spawning fish from December to April (Figure 3.7) verified this. Post-ovulatory follicles and/or hydrated eggs were noted in October, November, December and January. The latter feature was observed both in histological sections and while sampling fish. The size of ripe ovaries in the spawning season was much greater than that of testes (Figure 3.8).

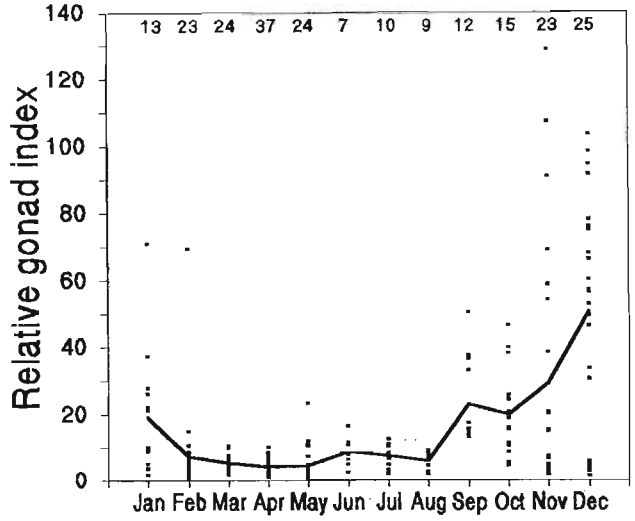


Figure 3.6: Monthly gonad indices for *E. andersoni* from the northern sampling region. The line joins the monthly means. Monthly data were pooled from May 1995 to September 1997. Monthly sample sizes are shown on top of the graph.

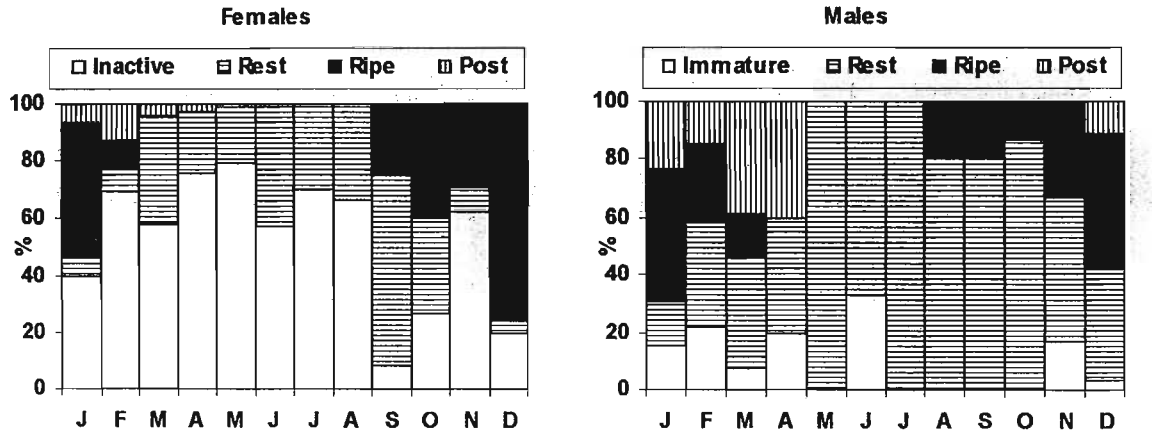


Figure 3.7: Relative monthly percentages of each gonad stage in *E. andersoni* from the northern sampling region. Monthly data were pooled from May 1995 to September 1997 (Female n = 225; Male n = 151).

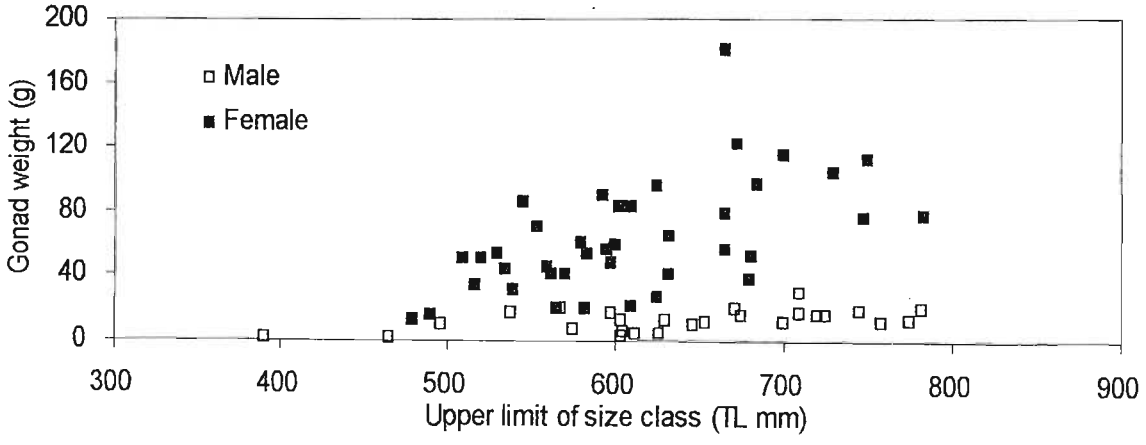


Figure 3.8: Plots of gonad weight for *E. andersoni* from the northern sampling region, during the spawning season (September to January). Data were pooled from May 1995 to September 1997.

Unusual catches

On one sampling trip on 5 February 1996, one commercial boat from the northern sampling region made an unusually large catch of rockcod (137 individual fish), most of which consisted of *E. andersoni* (n = 125). The average number of *E. andersoni* caught per commercial outing is typically 7.3 (SD 7.7) The unusually large catch was made over a 10-hour period and at a fairly consistent depth. The catch was made while the boat was undertaking a long, slow drift over an extensive, flat, reef area, i.e. the fish were not caught in a confined area. Another boat, operating in the same area, also caught an unusually large number of this species (approximately 60 fish) on the same day. Sixty-six of the fish from the former catch were sampled at random. Most were sexually active males, although inactive fish were also numerous (Table 3.4). The size range of these fish included both very small and very large specimens (Figure 3.9). On two other occasions, both in the month of January, but in different years, information was received that other "bumper" catches of *E. andersoni* had been made. One catch comprised about 90 fish, the other about 140 fish (estimated from reported catch weights). Unfortunately, no further details on these catches are available.

Table 3.4: Numbers in each reproductive stage of fish that were part of a large catch of *E. andersoni* made on 5 February 1996 in the northern sampling region by a commercial fisher. One inactive, bisexual fish was also recorded. Total n = 66.

Sex		Resting	Ripe	Post-spawning
F	17 (Inactive)	2	2	3
M	10 (Immature)	2	16	13

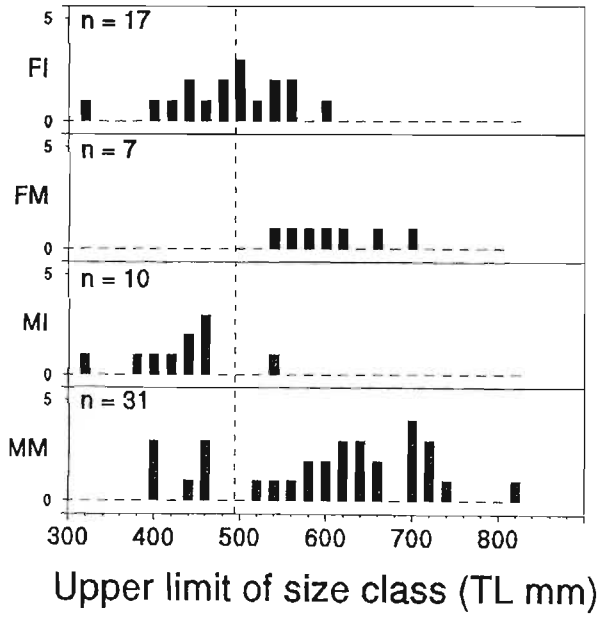


Figure 3.9: Length frequencies (by number) of *E. andersoni* from an unusually large catch made in the northern sampling site (5 February 1996). FI = inactive female, FM = mature female, MI = immature male, MM = mature male. The dashed vertical line signifies length at 50% maturity in females.

Size at sex change

Sex-changing individuals, i.e. with both mature male and mature or maturing female tissues, ranged in length from 550 mm to 670 mm. The method of Shapiro (1987) for determining size at sex change in protogynist species is inappropriate for *E. andersoni*, as the lengths of males and females overlap completely.

Size at maturity

Minimum lengths at maturity were 417 mm and 383 mm for females and males, respectively. Using the fitted curve, length at 50% maturity in females was estimated at 492 mm (Figure 3.10), but could not be estimated for males because of a paucity of immature fish of this sex in samples during the spawning season. Because of the difficulty in differentiating between inactive, mature fish and immature fish (see description of inactive female gonad stage), and assuming that all inactive fish larger than the minimum size at maturity are, in fact, mature, length at 50% maturity in females could be as low as 430 mm.

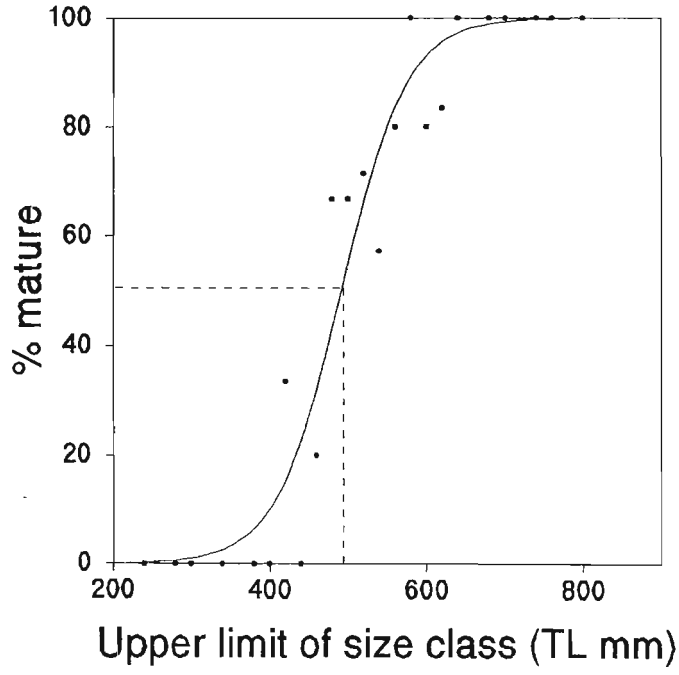


Figure 3.10: Length at 50 % maturity estimated for female *E. andersoni* from the northern sampling region during the spawning season.

Discussion

E. andersoni exhibits several of the characteristics listed by Sadovy and Shapiro (1987) as being indicative of protogynous hermaphroditism. There is a lamellar structure and a lumen in both male and female gonads, and the lumen is not used for the transport of sperm in males. Instead, sperm is transported in sinuses that develop in the gonad wall. Also occurring are transitional gonads that had previously functioned as females, evidenced by atresia of vitellogenic oocytes, and that are in the process of becoming active males i.e. with various stages of sperm development. However, two characteristics of monandric protogyny viz. a bimodal size frequency (with males generally being larger than females), and a female-

biased sex ratio, are not apparent. In *E. andersoni*, there is a complete overlap of mature male and female size frequencies, their mean sizes are very similar and males significantly outnumber females. Similar sizes of the sexes is more characteristic of gonochorist or diandric protogynous species (Sadovy and Colin, 1995), while a male-biased sex ratio suggests protandry (Sadovy and Shapiro, 1987). Although the observations for *E. andersoni* were made in fish sampled from an exploited population, this should not detract from their validity, as similar-sized fish of both sexes should respond similarly to fishing pressure, unless the sexes are spatially segregated and there is greater fishing effort on one sex. Fishing is also unlikely to produce a male-biased sex ratio in monandric protogynists, since the larger males are generally removed first (Bannerot *et al.*, 1987).

A further criterion for gonochorism is that the majority of individuals function as either male or female in their lifetime, not both (Sadovy and Shapiro, 1987; Sadovy, 1996). In *E. andersoni*, males can develop directly from immature females, evidenced by the occurrence of four mature males at sizes smaller than the smallest mature female. Combined with the other length frequency data, this suggests that *E. andersoni* could be classified as a functional gonochorist. However, the existence of a few individuals with mature elements of both male and female tissue suggests that at least some part of the population functions as a female and then as a male i.e. undergo functional protogynous sex change. The situation may be clarified by referring to the following schematic (Figure 3.11).

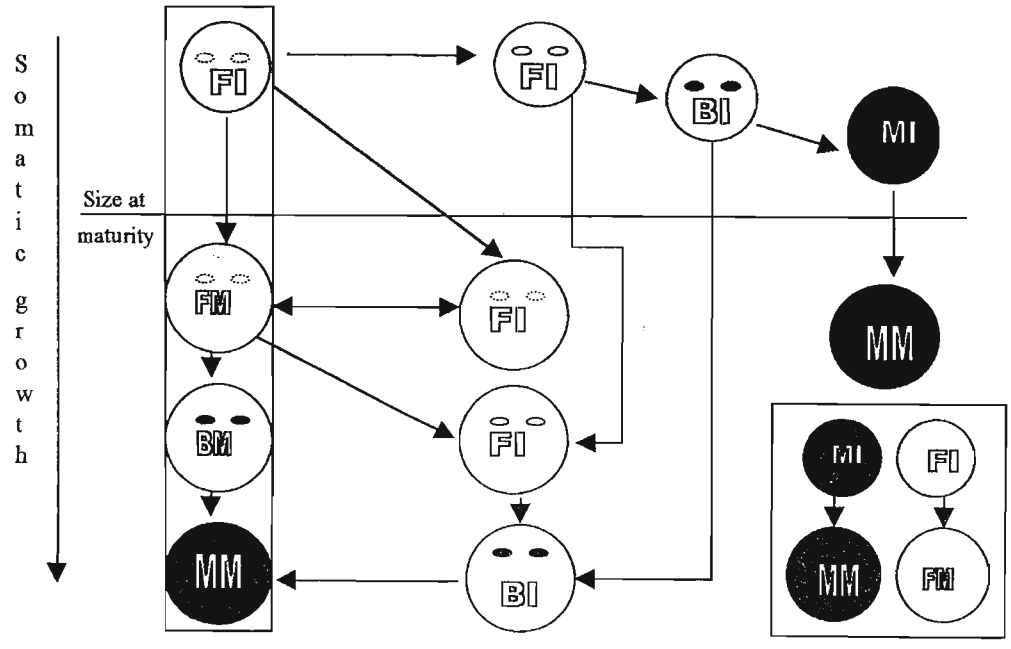


Figure 3.11: Schematic of potential gonad ontogeny in *E. andersoni*. The large circles represent cross-sections through gonads, and the smaller ovals represent precursor cells (dotted ovals), presumptive male tissue i.e. spermatogonia (clear ovals) and spermatocytes (black ovals) respectively. BI = inactive bisexual, BM = mature bisexual (transitional), FI = inactive female, FM = mature female, MI = immature male, MM = mature male. The rectangular box represents typical monandric protogynous hermaphroditism in serranids, the lower right box represents gonochorism.

All gonads commence ontogeny as immature females (FI). At a size of between 350 mm and 400 mm, some of these gonads develop a clearly distinguishable (at the light microscope level) area of presumptive male tissue (spermatogonia) in the region of the dorsal blood vessel. It is likely that the precursor cells to these spermatogonia are present in all FI gonads, only some of which become bisexual. Such hypothesized precursor cells were not identified in this study, probably because they were very small and isolated. The presumptive tissue itself is only recognisable once it has proliferated in the region of the blood vessel.

FI gonads can either remain inactive as the fish grows (accounting for FI gonads in large fish), or they mature. Some result in small females with mature ovaries (FM), while for FI gonads with presumptive male tissue, the previtellogenic oocytes remain quiescent, and the presumptive male tissue either develops rapidly or slowly. If development is rapid, spermatocytes are produced early on, accounting for bisexual gonads (BI) in small fish. These gonads develop into immature testes (MI) in small males and then into mature testes (MM). If development of the presumptive tissue is slow or delayed, there is substantial somatic growth before the spermatocytes appear, accounting for the FI gonads with presumptive tissue in large fish.

Returning to the mature female (FM) gonads, three subsequent alternatives are possible. Firstly, the gonad continues to function as an ovary as the fish grows, accounting for the large, mature females (FM). Secondly, in some of these gonads, the precursor tissue develops into presumptive tissue, and the gonad subsequently undergoes transition, with the maturing/mature female tissue regressing and being replaced by male tissue – these are the BM gonads. These gonads ultimately become mature testes (MM) in large fish. Thirdly, the FM gonads in large fish may regress to an FI stage (still retaining the precursor tissue), which would account for the FIs in large fish. Some of these ovaries may ripen again, and others subsequently become BI gonads if the male tissue develops. This constitutes an alternative origin for bisexual inactive gonads in large fish. These BI gonads, in turn, develop into mature male gonads. This third alternative cannot be refuted based on the available evidence. In both of these last two options, the gonads must retain the potential to develop male tissue, although in a form not identified in this study e.g. as tiny cysts of bipotential gonia. Note that, although all possible developmental routes have been depicted here, they may not necessarily all occur.

It is difficult to determine what proportion of males are derived via the immature female or mature female routes. Since there are significantly more mature males than mature females, this suggests that a considerable proportion of males arise via the immature female route. The predominance of mature males and BIs in size classes less than the female size at 50% maturity indicates that the majority of these probably arise directly from the immature female phase, at least for these size classes. One could also potentially expect greater numbers of BIs in the larger size classes if these gonads mostly arose via the mature female route. This suggests that the main origin of males is via the immature female route, with some fish retaining the potential for protogynous sex change.

Despite the serial sectioning, it is possible that the FI fish with presumptive male areas are, in fact, BIs, but were mis-classified as FI because no spermatocytes were observed. Also despite the efforts to locate it, presumptive tissue in FI fish may have

been overlooked if it was very localised. The effect of the former problem would be to increase the proportion of BI fish observed (Figure 3.1.2), while the effect of the latter would be to increase the proportions of fish with presumptive tissue (Figure 3.1.1).

The age information presented in chapter 4 also provides evidence that not all males are derived from mature females, and is briefly discussed here in order to clarify the sexual pattern. Although the youngest age classes consisted of immature females, young males were also observed, and the male age at first maturity was lower than the female age at first maturity. Moreover, immature bisexuals were recorded at lower ages than the female age at first maturity, indicating that some males develop from immature females. Apart from the young fish (< 3 years), there was complete overlap in ages of females and males, and males were not more numerous in the older age classes than females. These observations show that males can develop directly from juvenile females. Serranids are thought to have evolved from a protogynous ancestor (Smith, 1967), so in *E. andersoni*, the partial reversion to gonochorism may be termed secondary gonochorism (Smith, 1975). However, the occurrence of fish in transition from mature female to male indicates that this is an alternative route for males, and hence *E. andersoni* is best classified as a diandric protogynous hermaphrodite.

The functional significance of the inactive bisexual phase could not be completely resolved. Many of the inactive bisexual fish were larger than the minimum size of sexual maturation, and were clearly inactive even during the reproductive season. It could not be determined in these fish whether (a) they had previously spawned as females and the gonad had regressed to an non-spawning condition which persisted (as for inactive females, it is clear that mature-sized inactive bisexuals do not spawn every year, if they have spawned at all: for both of these categories, the large-sized individuals may spawn intermittently as females and regress to a non-spawning phase for certain years), or (b) sexual maturation was delayed in certain individuals until they reached some threshold size.

In support of the former possibility, some individuals in certain species are known not to spawn every year e.g. females of the sparid, *Acanthopagrus australis* (Pollock, 1984), although in this species the ovaries develop to an advanced stage before regressing. Tilney (1990) also reported non-spawning in the ariid, *Galeichthyes feliceps*, and suggested that this was a result of non-availability of males during the spawning season. More relevantly, Koenig *et al.* (1996) showed that some mature females of a serranid, *Mycteroperca microlepis*, remained inactive during the spawning season. In this species, the inactive females remained inshore in shallow water, while the reproductively active fish moved into deeper water to join a spawning aggregation. Insufficient information exists to suggest a similar scenario in *E. andersoni*. A plot of capture depth against fish length for inactive, resting and ripe fish in the spawning season showed some restriction of the inactive females to shallower depths, but this was not conclusive. However, on at least one sampling occasion, mature-sized fish that had been caught in one locality were all found to be reproductively inactive, while fish caught at another near-by locality on the same day were in a ripe condition. Greater resolution in capture locality information is required to resolve whether there are spatial differences in reproductive activity.

E. andersoni is endemic to the coast of southeast Africa (Figure 3.12), so the southern sampling region is located towards the southern limit of the distributional range of this species. The predominance of reproductively inactive fish in the southern sampling region suggests that some environmental factor in the region precludes spawning there. Alternatively, mature fish could be migrating northwards to spawn, thereby ensuring that the larvae are dispersed southwards. This phenomenon has been reported for reef-associated fishes from other families

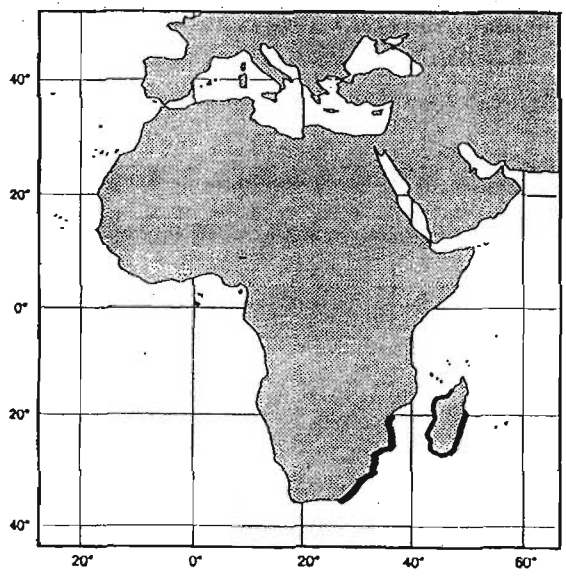


Figure 3.12: Distribution of *E. andersoni* (from Heemstra and Randall, 1993).

Description of gonad stages - E. rivulatus

Immature female (n = 18; Figure 3.13a)
These gonads contained gonia and closely-packed, previtellogenic oocytes. There were no indications of prior spawning in gonads of 8 fish that were larger than the female size at 50% maturity (219 mm). Three of these were relatively large (TL 254 mm, 258 mm, 323 mm), showed no signs of reproductive activity in the spawning season, and should therefore probably be designated as inactive female gonads.

Mature, resting female (n = 97; Figure 3.13b)
Previtellogenic and cortical alveolar oocytes were present. All resting gonads exhibited signs of prior spawning in the form of prominent muscle bundles that were particularly prominent shortly after the spawning season (Figure 3.13.1). There were two types of bundles, namely intralamellar bundles, and "wall" bundles i.e. those that formed part of the gonad wall. In an individual gonad, both or either occurred. Only well-developed bundles were used as an indicator of previous spawning. Large melano-macrophages occurred in most of these gonads. Six gonads had a few (< 5) isolated, scattered cysts of stage 1 or 2 spermatocytes.

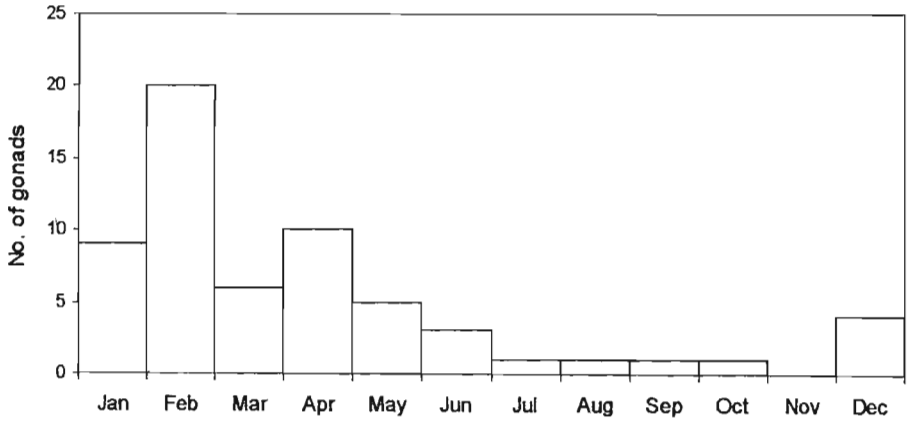


Figure 3.13.1: Monthly occurrence of mature, resting, female *E. rivulatus* gonads with intralamellar muscle bundles. Northern and southern sampling regions combined; monthly data from May 1995 to September 1997 are pooled.

Mature, ripe female (n = 63; Figure 3.13c)
Gonads were substantially larger than those in a resting stage, and contained previtellogenic and cortical alveolar oocytes, as well as many vitellogenic oocytes. Four of these gonads had a few (< 5) isolated, scattered cysts of stage 1 or 2 spermatocytes. Gonads of this stage were recorded from both northern and southern sampling regions. Hydrated eggs and/or post-ovulatory follicles were observed in August, September, October and November.

Post-spawning female (n = 14; Figure 3.13d)
These gonads had numerous previtellogenic oocytes and showed widespread atresia of vitellogenic oocytes. The gonads generally had a disorganised appearance, with intralamellar spaces and cytoplasmic strands. One gonad had a few (< 5) isolated, scattered cysts of stage 1 or 2 spermatocytes. Small melano-macrophages occurred in all of these gonads.

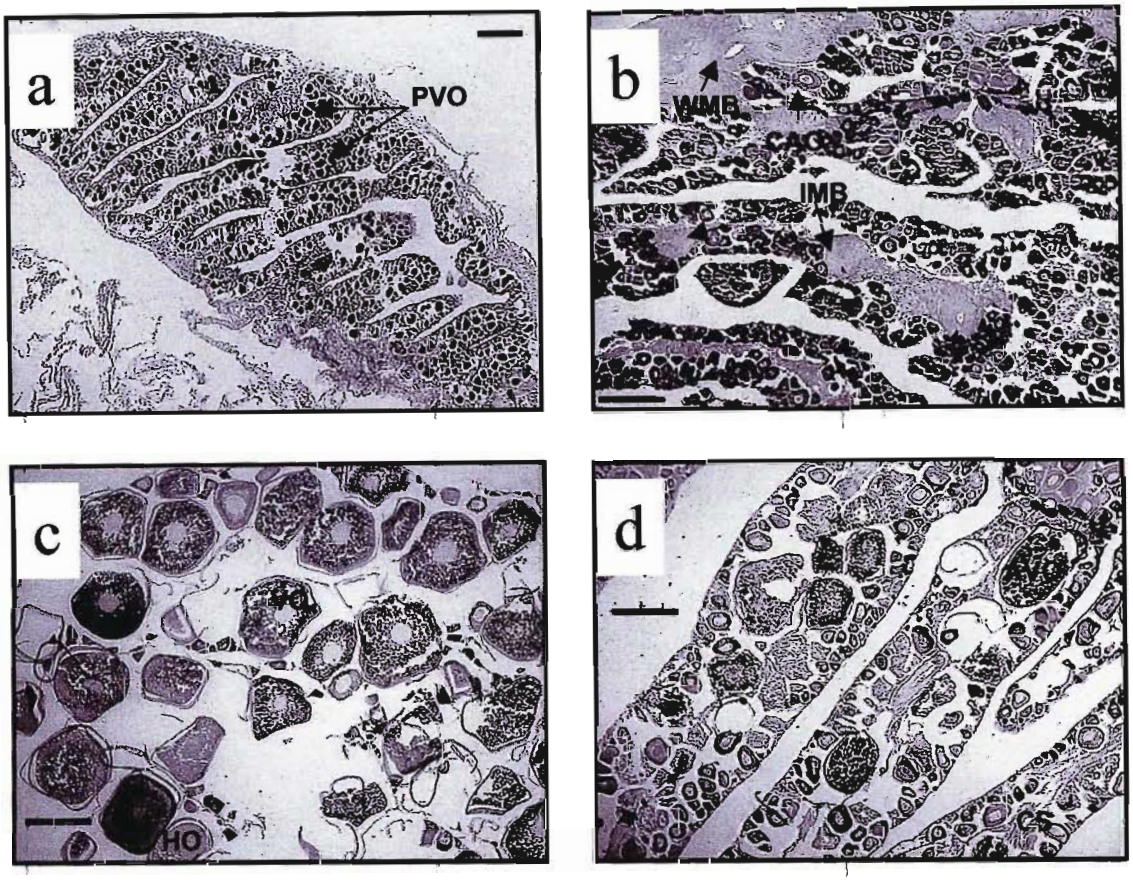


Figure 3.13: Cross-sections of female *E. rivulatus* gonads.

a Immature female gonad showing lamellar structure and previtellogenic oocytes (PVO). TL 138 mm, May 1996. Scale bar = 100μ.

b Mature, resting, female gonad showing muscle bundles ("wall" bundles (WMB) and intralamellar bundles (IMB)) and cortical alveolar oocytes (CAO). TL 302 mm, January 1996. Scale bar = 300μ.

c Ripe female gonad showing vitellogenic oocytes (VO) and an early hydrated oocyte (HO). TL 299 mm, September 1995. Scale bar = 300μ.

d Post-spawning female gonad showing atretic, vitellogenic oocytes (AVO) and strands of connective tissue (CS). TL 291 mm, September 1995. Scale bar = 300μ.

Transitional (n = 6; Figure 3.14a-d)
These gonads contained large numbers of previtellogenic oocytes, with varying amounts of male tissue. The male tissue ranged from scattered cysts of spermatocytes, to a combination of isolated cysts and aggregated clusters of cysts that were more numerous in lamellae proximal to the dorsal blood vessel (Figure 3.14c). The extent of the male tissue ranged from 20 to 30 cysts in one gonad, to a gonad in which the proportions of male and female tissue were approximately equal. All six gonads showed signs of prior female function in the form of muscle bundles, and one gonad also had atretic cortical alveolar oocytes (Figure 3.14d). These characteristics indicate prior female function and development to a functional male. Gonads in the process of changing sex were recorded in February, March, April and May.

Immature male (n = 1; Figure 3.15a)
This gonad was small, and consisted exclusively of spermatogonia and early stages of spermatocytes. No sperm was observed and no sperm sinuses had developed.

Mature, resting male (n = 102; Figure 3.15b)
Most of the gonad consisted of stage 1 and 2 spermatocytes, with occasional cysts of sperm. In some gonads, small amounts of sperm were also scattered within the sperm sinuses or loosely within lobules. Stage 1 and 2 oocytes were often present (n = 16; 16 % of male gonads in this stage), were scattered throughout the lamellae, and were occasionally numerous. Muscle bundles (intralamellar and/or wall bundles) occurred in 10 resting male gonads, and eight of these gonads also had several previtellogenic oocytes. Large melano-macrophages (brown bodies) commonly occurred.

Mature, ripe male (n = 78; Figure 3.15c)
Stage 1 and 2 spermatocytes were present, but the gonads were dominated by later stages of spermatogenesis. Sperm were present in both the lobules and the sperm sinuses. In some, the lobule walls had split and large areas of sperm were evident. Sperm were never observed in the gonadal lumen. Stage 1 and 2 oocytes were also present in ripe male gonads (n = 16; 20 % of male gonads in this stage). Ten gonads had intralamellar and/or wall bundles, and of these, 5 had previtellogenic oocytes.

Post-spawning male (n = 25; Figure 3.15d)
These gonads consisted mostly or entirely of seminiferous tubules, sometimes with a few cysts of spermatocytes, and varying amounts of sperm still contained in the sinuses. The gonads often had thick, muscular walls, and the lamellae were often disrupted with large empty spaces. One post-spawning gonad had previtellogenic oocytes and two others had muscle bundles. Large melano-macrophages (brown bodies) occurred in most of these gonads.

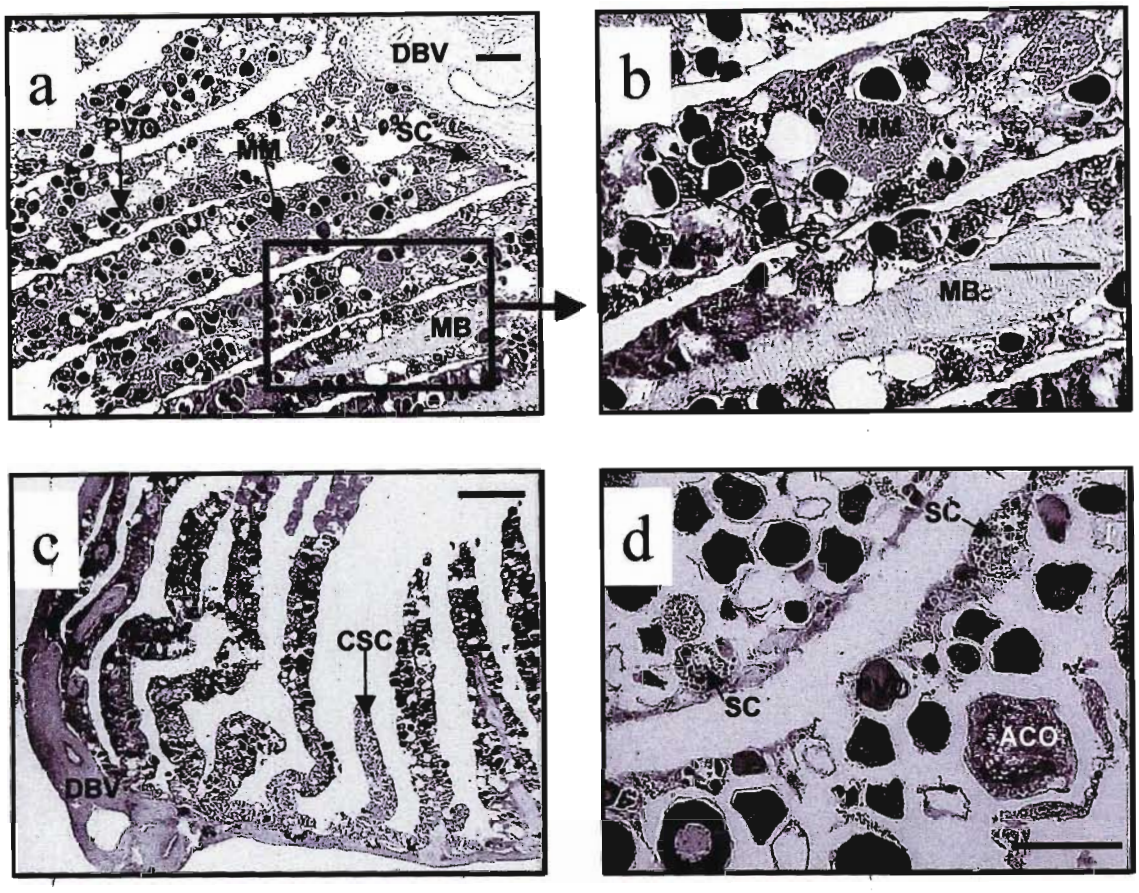


Figure 3.14: Cross-sections of transitional *E. rivulatus* gonads.

a Section of a gonad showing lamellae containing previtellogenic oocytes (PVO), cysts of spermatocytes (SC) and melano-macrophages (MM). Dorsal blood vessel (DBV) also shown. TL 349 mm, February 1996. Scale bar = 300μ.

b Magnified view of (a), showing previtellogenic oocytes (PVO), cysts of spermatocytes (SC) and melano-macrophages (MM). Scale bar = 100μ.

c Section of a gonad showing clusters of cysts of spermatocytes (CSC) that are more abundant near the dorsal blood vessel (DBV). TL 272 mm, March 1996. Scale bar = 100μ.

d Section of a gonad showing cysts of spermatocytes (SC), previtellogenic oocytes (PVO) and an atretic, cortical alveolus stage oocyte (ACO). TL 305 mm, May 1996. Scale bar = 100μ

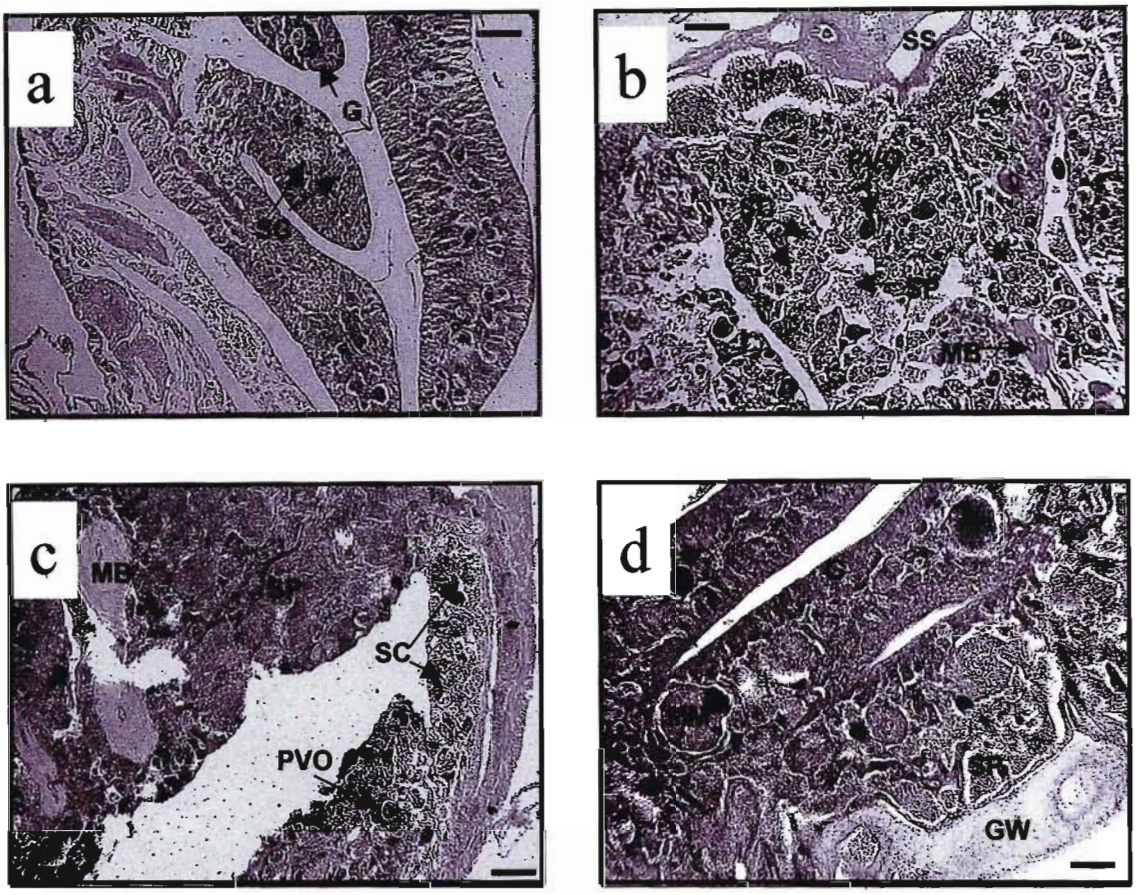


Figure 3.15: Cross-sections of male *E. rivulatus* gonads.

a Immature, male gonad, showing cysts of spermatogonia (G) and spermatocysts (SC). TL 235 mm, June 1995. Scale bar = 100μ.

b Mature, resting, male gonad, showing scattered previtellogenic oocytes (PVO), cysts of spermatocytes (SC), sperm (SP), a sperm sinus (SS) and muscle bundles (MB). TL 271 mm, September 1995. Scale bar = 100μ.

c Ripe, male gonad, showing aggregations of sperm (SP), muscle bundles (MB), spermatocytes (SC) and scattered previtellogenic oocytes (PVO). TL 290 mm, September 1995. Scale bar = 100μ.

d Post-spawning, male gonad, showing clusters of sperm (SP), gonia (G), melano-macrophages (MM) and the thickened gonad wall (GW). Tl 306 mm, January 1995. Scale bar = 100μ.

Length frequencies and sex ratios

Length frequency histograms of the various sex and maturity stages (Figure 3.16) showed that immature fish were seldom encountered in either sampling region. The smallest size classes consisted of immature females, and mature males were more common in the larger size classes.

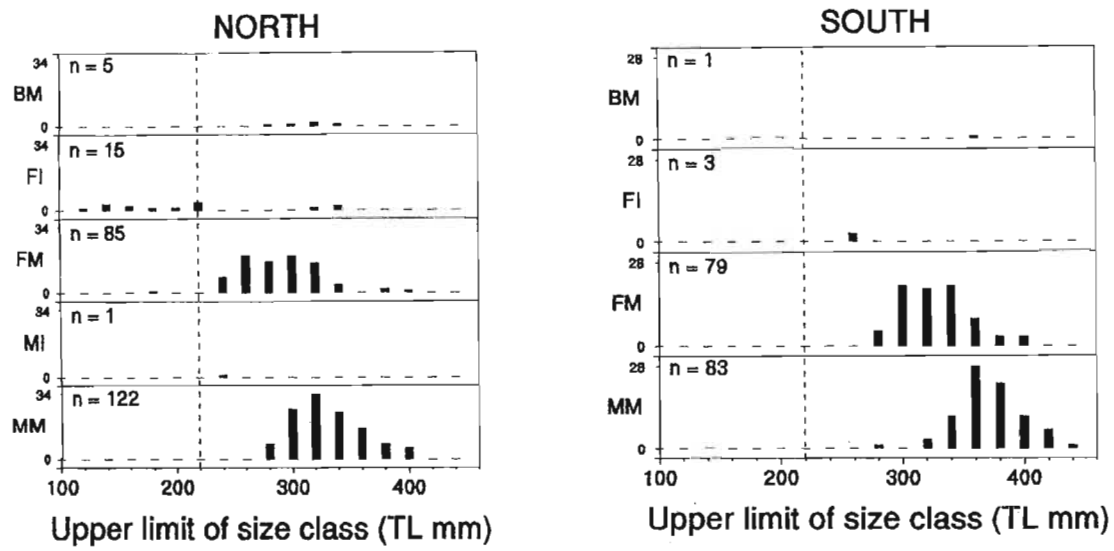


Figure 3.16: Length frequencies (by number) of *E. rivulatus* from northern and southern sampling sites. BM = mature bisexual (transitional), FI = immature female, FM = mature female, MI = immature male, MM = mature male. The dashed vertical line indicates length at 50% maturity in females.

Because reproductive activity occurred in the majority of fish from both northern and southern sampling regions, comparisons of lengths and sex ratios of mature fish were based on the combined samples from both regions. Mature males ranged in size from 261 mm to 435 mm, females from 165 mm to 390 mm, and their mean sizes (338 mm (SD 34) and 298 mm (SD 37), respectively) were significantly different ($t = 10.9$, $DF = 367$, $p < 0.001$). Overall, mature males significantly outnumbered mature females (1.25 : 1, $n = 369$, $\chi^2 = 4.56$, $p < 0.001$), although this was not the case in the southern sampling region, where the ratio was 1:1.

Spawning season

Peaks in gonad indices indicated that spawning season extended from July or August to November (Figure 3.17). The relative proportions of each gonad stage on a monthly basis and the appearance of post-spawning fish from December to February (Figure 3.18) verified this. Post-ovulatory follicles and/or hydrated oocytes were noted in August, September, October and November. The latter feature was observed both in histological sections and while gutting fish. The size of ripe ovaries in the spawning season was generally greater than that of testes (Figure 3.19).

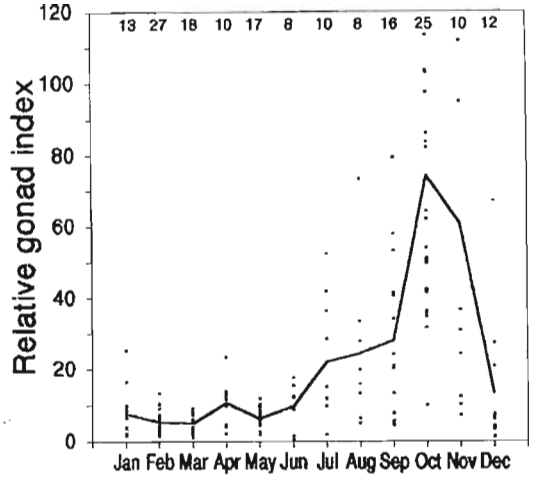


Figure 3.17: Monthly gonad indices for *E. rivulatus* from northern and southern sampling regions (May 1995 to September 1997). The line joins the monthly means. Monthly data were pooled from May 1995 to September 1997. Sample sizes are shown on top of the graph.

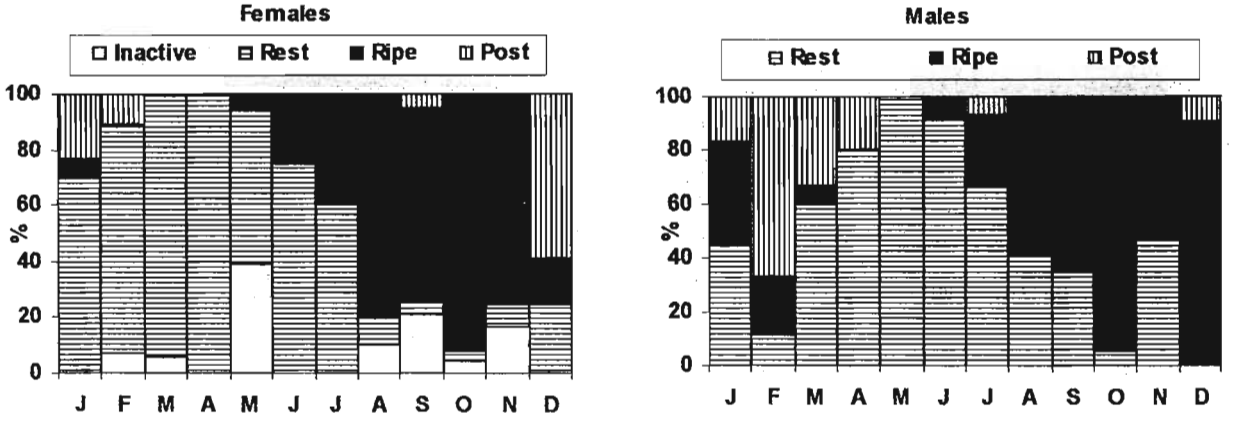


Figure 3.18: Relative monthly percentages s of gonad stages for *E. rivulatus* from the northern and southern sampling regions. Female n = 182, male n = 185. Monthly data were pooled from May 1995 to September 1997.

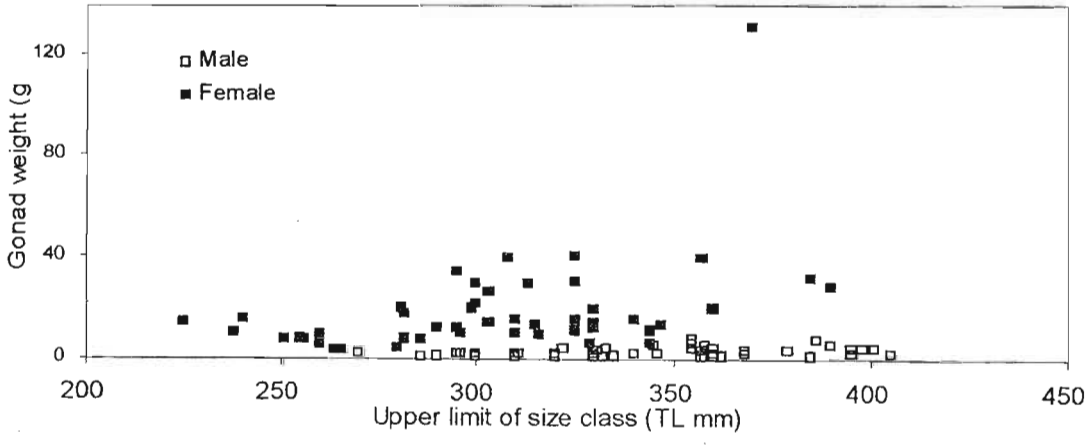


Figure 3.19: Plots of gonad weight for *E. rivulatus* during the spawning season (July to November). Data were pooled from May 1995 to September 1997.

Size at sex change

In samples from the southern sampling region, the length range between the smallest male (261 mm) and the largest female (390 mm) represented 29 % of maximum size. The median value of this range (340 mm) provides an estimate of the size at sex change (Shapiro, 1987). In the northern region, the length range between the smallest male (270 mm) and the largest female (390 mm) represented 28 % of maximum size, and the size at sex change was estimated to be 310 mm. These estimates were significantly different ($\chi^2 = 37.8$, $p < 0.001$)

Size at maturity

Minimum lengths at maturity were 165 mm for females and 261 mm for males respectively. Minimum size at maturity for females could be over-estimated, because the smallest mature fish observed (165 mm) was a captive fish, and the smallest, mature, "wild" fish had a length of 225 mm. Length at 50% maturity in females occurred at 219 mm (Figure 3.20), but could not be estimated for males because of a paucity of immature fish of this sex in samples collected during the spawning season. Class intervals of 50 mm had to be used (as opposed to the 20 mm intervals used for the other species) because of a paucity of fish less than 250 mm in length in samples, which would have resulted in an extremely steep maturity curve. If the three large inactive females fish included in the immature female stage are in fact mature, estimated length at 50% maturity in females is only slightly lower (218 mm).

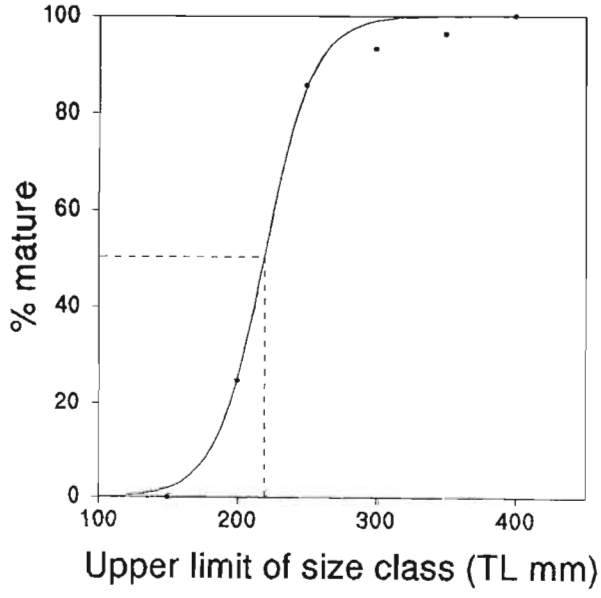


Figure 3.20: Length at 50 % maturity estimated for female *E. rivulatus* from the northern and southern sampling regions.

Discussion

Despite the low numbers of fish in the smaller size classes obtained in this study, there is strong evidence to suggest that *E. rivulatus* is a monandric protogynous hermaphrodite. Firstly, there is a bimodal size frequency, with males predominating

in the larger size classes and having a significantly larger mean size. The age information presented in chapter 4 also supports the potential for protogynous hermaphroditism. The youngest age classes comprised immature and mature females only, males were only observed at ages well above the female age at 50% maturity, and the older age classes were comprised entirely of males. Together, this information indicates that males are derived from mature females. The male-biased sex ratio is likely to be an artefact, since the fishery tends to target larger individuals and hence catches fewer small fish, implying that much of the female component is excluded from the catch.

Histological evidence for protogyny includes the occurrence in testes of a membrane-lined lumen and a lamellar structure, both of which indicate a possible previous female phase of development (but see General Discussion). The development of several sperm sinuses in the gonad wall for the transport of sperm in ripe males, as opposed to the distinct sperm duct found in gonochorists, also supports this argument. More significant is the occurrence of precocious cysts of spermatocytes in several female gonads and most female developmental stages. Strongest evidence is the occurrence of six transitional gonads with mature female tissue and maturing male tissue. The classification of the female part of these gonads as mature is based on the appearance of post-spawning muscle bundles, and, in one gonad, the occurrence of cortical alveolar stage oocytes. The appearance of these bundles in mature, resting ovaries shortly after the spawning season, arising from the contraction of the ovary after spawning, supports this classification (Shapiro *et al.*, 1993b). Although bundles were also recorded in male gonads, they occurred in both ripe and resting testes, and there was no particular seasonality in their appearance. The link between muscle bundles in testes and spawning by these gonads is thus not clear, and the appearance of bundles in gonads with mature male and female tissue is strong evidence of prior female functioning. Mackie (2000) also concluded that *E. rivulatus* from Western Australia is a protogynous hermaphrodite, based on gonad morphology, population structure and the occurrence of a single transitional gonad.

E. rivulatus is widely distributed in the Indo-Pacific, and, although largely tropical, the species also occurs at fairly high latitudes (> 30°) (Heemstra and Randall, 1993; Figure 3.21). In KwaZulu-Natal, this species spawns in both northern and southern sampling regions, evidenced by the occurrence of ripe ovaries and testes in fish from these areas. Despite being towards the end of its southern distribution, spawning of *E. rivulatus* seems unaffected by the lower sea temperatures in the southern sampling region. This is supported by evidence of spawning from July to November on the KwaZulu-Natal coast, when sea surface temperatures are at their lowest (Figure 2.2; Chapter 2). Mackie (2000) also recorded reproductive activity of this species during months when water temperatures were cooler (July to December) in Western Australia, Nzioka (1979) recorded ripe fish in October off Tanzania, and Morgans (1982) also noted that this species was tolerant of cooler water in Kenya.

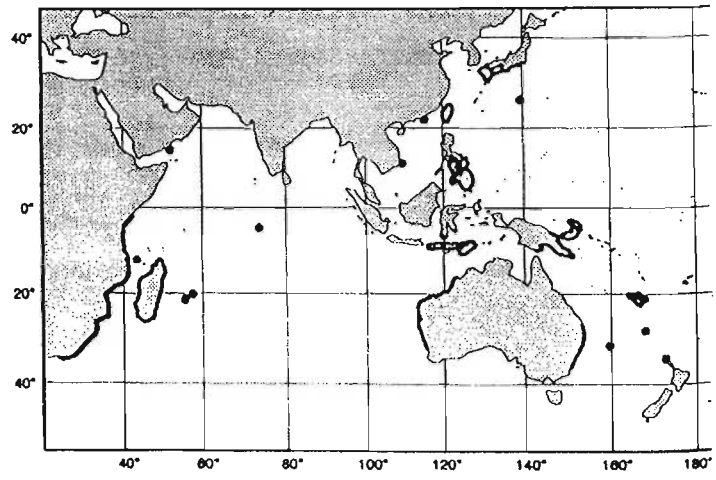


Figure 3.21: Distribution of *E. rivulatus* (from Heemstra and Randall, 1993).

The overlap in the length frequencies of mature males and females gives an indication of the size range over which sex change can occur (Shapiro, 1987). In this study, the length range between the smallest male and the largest female from both sampling regions represented a fairly high percentage (almost 30 %) of their maximum size. Size at sex change differed significantly between these areas. Mackie (2000) sampled *E. rivulatus* at several sites in Western Australia, and found that the range of male/female overlap as a percentage of maximum size varied between sites, ranging from 8 – 34 %. His estimates of size at sex change also varied significantly between sites, ranging from 263 mm to 315 mm, compared to the estimates of 310 mm and 340 mm obtained in this study. The fairly high degree of male/female size overlap and the variable estimates of size at sex change in both South Africa and Western Australia suggest that transition in *E. rivulatus* can occur over a wide range of female sizes or ages.

Mackie (2000) found slightly lower minimum sizes at maturity for male (221 mm) and females (144 mm), as well as a lower size at 50 % maturity for females (194 mm) than I did. The larger sizes estimated from South African waters may be as a result of the paucity of samples in the smaller size classes, or because of population-level differences. Mackie (2000) also obtained a significantly female-biased sex ratio, contrasting with the significantly male-biased ratios obtained in this study. His fish were mostly collected by research methods and not from the fishery, and therefore included a greater proportion of smaller (female) fish. Morgans (1982) also reported a female-biased sex ratio (M:F 1:8.75), and a smaller size at maturity for females (265 mm) than males (310 mm) in Kenyan samples of this species, although no indication was given as to whether sexes were determined by histological methods.

Description of gonad stages - E. marginatus

Immature female (n = 227; Figure 3.22a)
These gonads contained gonia and closely-packed, previtellogenic oocytes. Although most of these fish were small, and therefore probably immature, a few (n = 9; 4%) were larger than the female length at 50% maturity (635 mm TL). Two of these were substantially larger than the length at 50% maturity (TL 680 mm and 713 mm) and yet showed no signs of reproductive activity during the spawning season. One gonad had a few (<5) cysts of stage 1 spermatocytes.

Mature, resting female (n = 37; Figure 3.22b)
Previtellogenic and cortical alveolar oocytes were present. Several gonads exhibited signs of prior spawning in the form of prominent muscle bundles that were more common shortly after the spawning season (Figure 3.22.1). Only well-developed bundles were used as an indicator of previous spawning. Two gonads had a few (< 5) scattered cysts of stage 1 and 2 spermatocytes. Both of these gonads had a disrupted appearance, with intralamellar spaces, several early cortical alveolar stage oocytes, numerous melano-macrophages, as well as prominent muscle bundles.

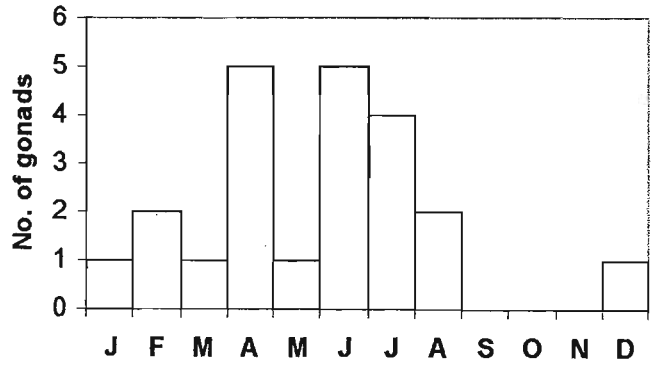


Figure 3.22.1: Monthly occurrence of mature, resting, female *E. marginatus* gonads with muscle bundles. Northern and southern sampling regions combined; monthly data from May 1995 to September 1997 are pooled.

Mature, ripe female (n = 40; Figure 3.22c)
Ovaries were substantially larger than those in a resting stage, and contained previtellogenic and cortical alveolar oocytes, as well as many vitellogenic oocytes. Post-ovulatory follicles were observed in one ripe ovary collected in November.

Post-spawning female (n = 2; Figure 3.22d)
These gonads showed widespread atresia of vitellogenic oocytes and had a disorganised appearance, with intralamellar spaces and cytoplasmic strands. Previtellogenic oocytes were also numerous.

Inactive bisexual (n = 1; Figure 3.23a)
Only one of these gonads was recorded, in a fish from the Mozambican samples. Previtellogenic oocytes and several stages of spermatogenesis, up to and including the spermatid stage, occurred in equal proportions. There were also several muscle bundles and melano-macrophages.

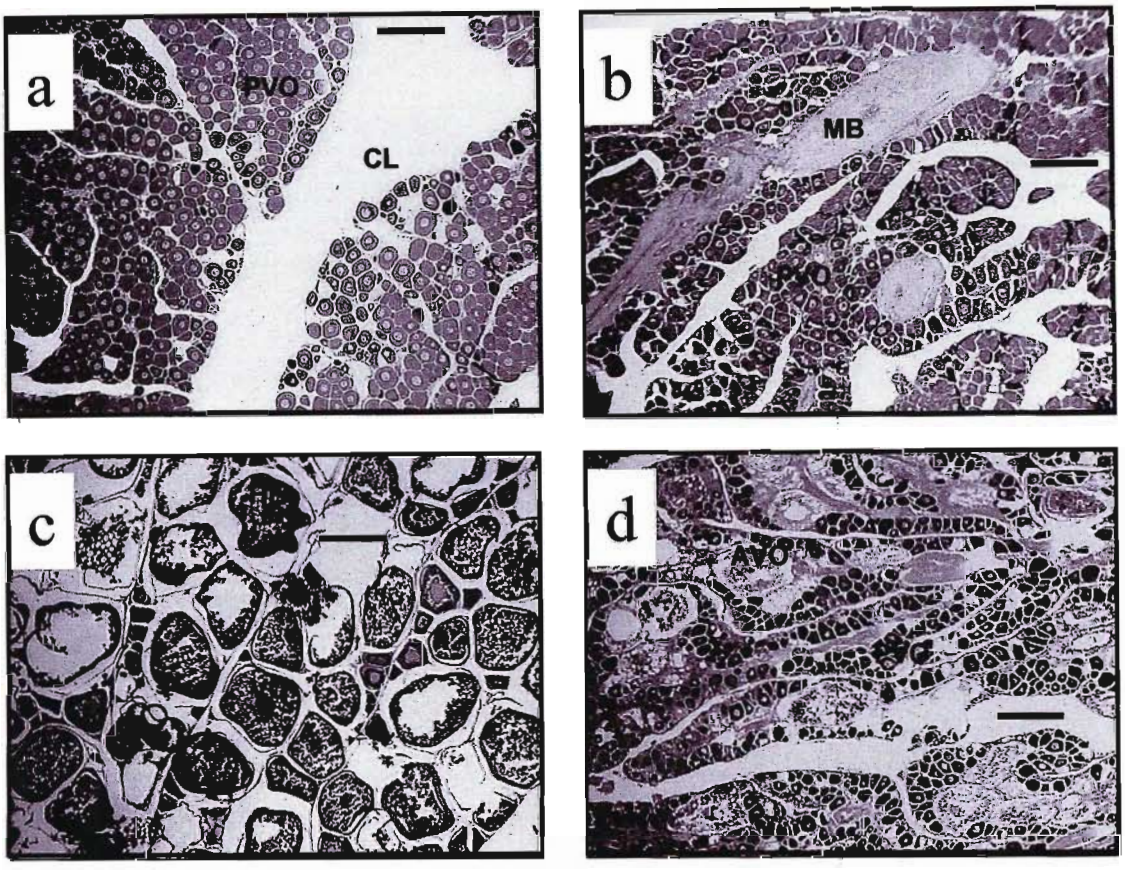


Figure 3.22: Cross-sections of female *E. marginatus* gonads.

a Immature, female gonad, showing previtellogenic oocytes (PVO) and the central lumen (CL). TL 475 mm, September 1995. Scale bar = 300μ.

b Mature, resting, female gonad, showing previtellogenic oocytes (PVO) and muscle bundles (MB). TL 701 mm, February 1995. Scale bar = 300μ.

c Ripe, female gonad showing vitellogenic oocytes (VO) and an hydrated egg (HE). TL 585 mm, October 1995. Scale bar = 300μ.

d Post-spawning, female gonad showing atretic, vitellogenic oocytes (AVO) and previtellogenic oocytes (PVO). TL 645 mm, February 1996. Scale bar = 300μ.

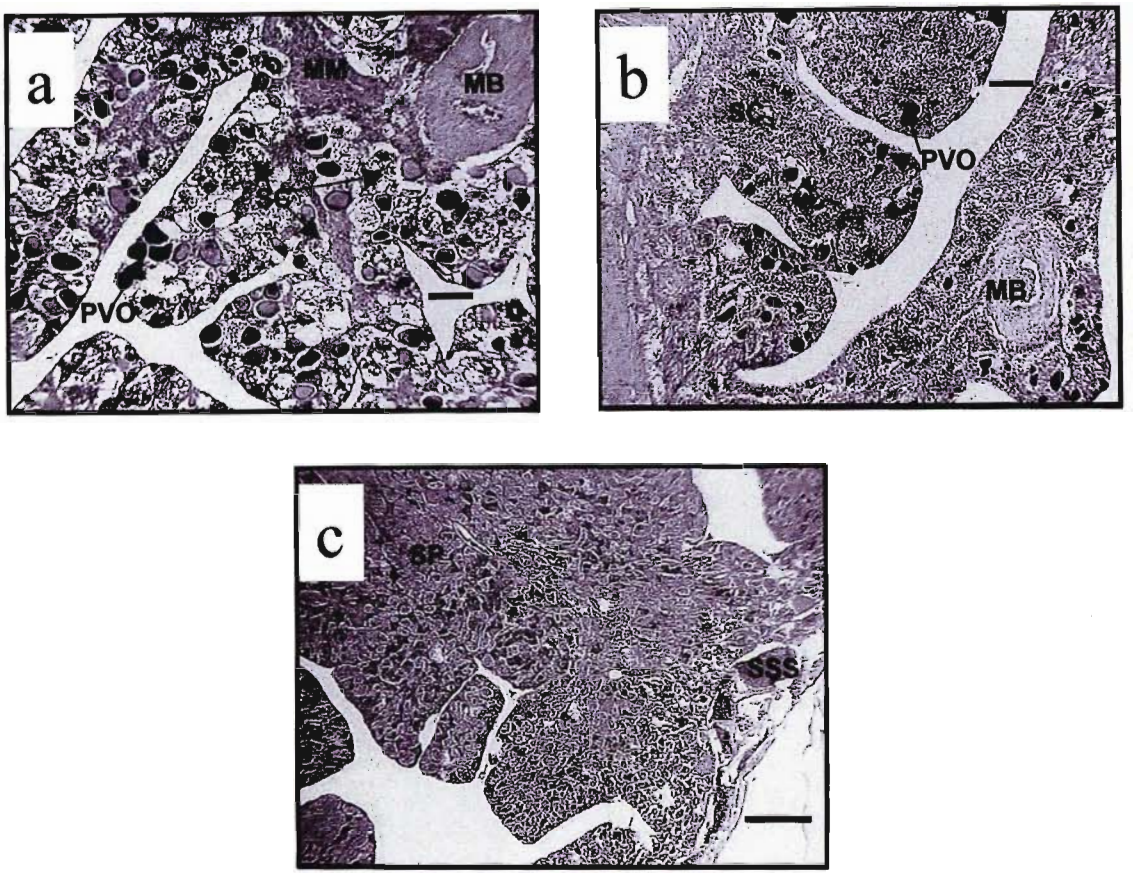


Figure 3.23: Cross-sections of *E. marginatus* gonads.

a Inactive bisexual gonad, showing numerous previtellogenic oocytes (PVO), cysts of spermatocytes (SC), muscle bundles (MB) and melano-macrophages (MM). TL 800 mm, September 1995. Scale bar = 100μ.

b Resting, male gonad, with a majority of cysts of spermatocytes (SC), scattered previtellogenic oocytes (PVO) and muscle bundles (MB). TL 800 mm, April 1996. Scale bar = 100μ.

c Ripe, male gonad, showing a mass of sperm (SP) in the lobules and in a sperm sinus (SSS). TL 970 mm, September 1996. Scale bar = 300μ.

Mature, resting male (n = 10; Figure 3.23b)
Most of the gonad consisted of spermatogonia and stage 1 and 2 spermatocytes, with occasional cysts of sperm either in the sperm sinuses or loosely within lobules. Previtellogenic oocytes occurred in three of these gonads, and in one gonad, they were numerous. This gonad, which was collected shortly after the spawning season in April 1996, also had well-developed muscle bundles, which suggests previous functioning as a female. Large melano-macrophages occurred in most of these gonads.

Mature, ripe male (n = 4; Figure 3.23c)
Stage 1 and 2 spermatocytes occurred, but the gonads were dominated by later stages of spermatogenesis. Sperm were present in both the lobules and the sperm sinuses. In some, the lobule walls had collapsed, and large areas of amalgamated sperm were evident. Sperm were not observed in the gonadal lumen. Melano-macrophages occurred in all four gonads.

Length frequencies and sex ratios

Length frequency histograms of the various sex and maturity stages (Figure 3.24) showed that immature female fish were common in samples from South African waters, particularly in the southern sampling region. Mozambican samples were dominated by mature fish, although it is not known if the collected samples were fully representative of the landed catch. The smallest size classes in both South African and Mozambican samples consisted of immature females, and in South African samples, mature males were restricted to the largest size classes.

Because the majority of fish larger than the female size at 50% maturity were mature in both northern and southern sampling regions, comparisons of lengths and sex ratios of mature fish were based on the combined samples from both of these regions. Mature males ranged in length from 800 mm to 1100 mm, females from 545 mm to 950 mm, and their mean sizes (917 mm and 709 mm, respectively) were significantly different ($t = 8.1$, $DF = 88$, $p < 0.001$). Mature males were significantly outnumbered by mature females (0.18 : 1, $n = 91$, $\chi^2 = 43.6$, $p < 0.001$).

Of the samples from Mozambican waters, mature males ranged in length from 670 mm to 910 mm, females from 560 mm to 880 mm, and their mean sizes (785 mm and 695 mm, respectively) were significantly different ($t = 4.7$, $DF = 55$, $p < 0.001$). Numbers of mature males and females were close to unity (0.90 : 1, $n = 59$, $\chi^2 = 0.15$, $p = 0.05$).

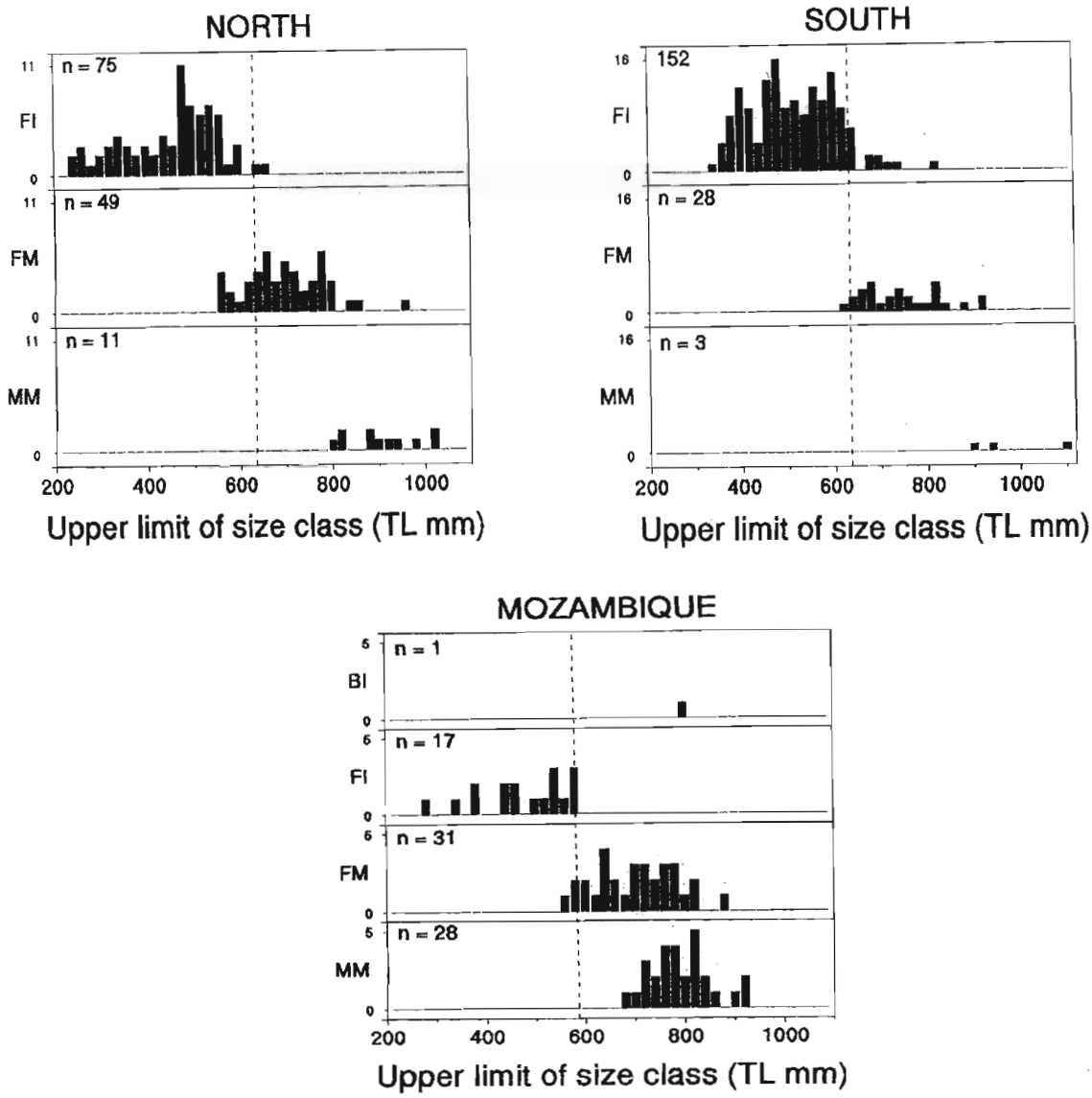


Figure 3.24: Length frequencies (by number) of *E. marginatus* from northern and southern sampling sites in KwaZulu-Natal, and Mozambique. BI = inactive bisexual, FI = immature female, FM = mature female, MM = mature male. The dashed line signifies length at 50% maturity in females.

Spawning season

Peaks in gonad indices (Figure 3.25) and plots of monthly gonad stages (Figure 3.26) indicated that spawning season was extended, with most spawning probably occurring from October to February (spring and summer). Low numbers of mature fish precluded a more precise determination of spawning season. Equivalent plots for males, and plots of relative gonad size, were not done because of low numbers. Histology revealed ripe males to be present in September, December and February, and hydrated eggs were noted in December, November and January. Low numbers of samples precluded the determination of spawning season in Mozambican waters. Histological sections of Mozambican fish revealed ripe fish in February, March, August, October and December (females) and February, March, June, October and November (males), which also suggests a prolonged spawning period. The sizes of ripe ovaries in these fish were generally greater than that of ripe testes (Figure 3.27).

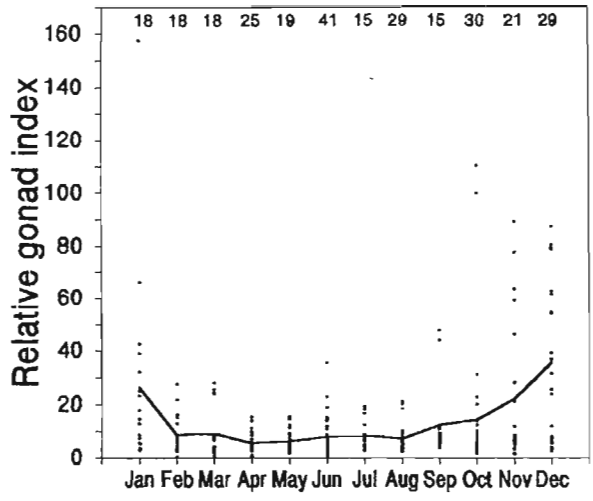


Figure 3.25: Monthly gonad indices for female *E. marginatus* from northern and southern sampling areas in KwaZulu-Natal (May 1995 to September 1997). The line joins the monthly means. Monthly data were pooled from May 1995 to September 1997. Monthly sample sizes are shown on the top of the graph.

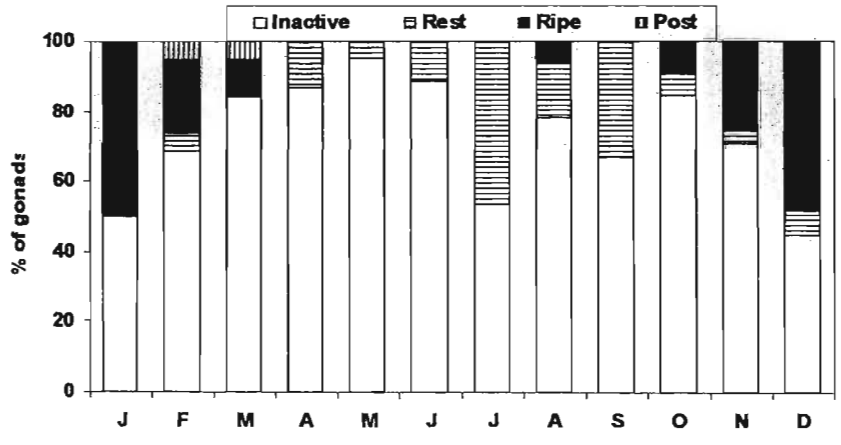


Figure 3.26: Relative monthly percentages of gonad stages for female *E. marginatus* from northern and southern sampling areas in KwaZulu-Natal (n = 301). Monthly data were pooled from May 1995 to September 1997.

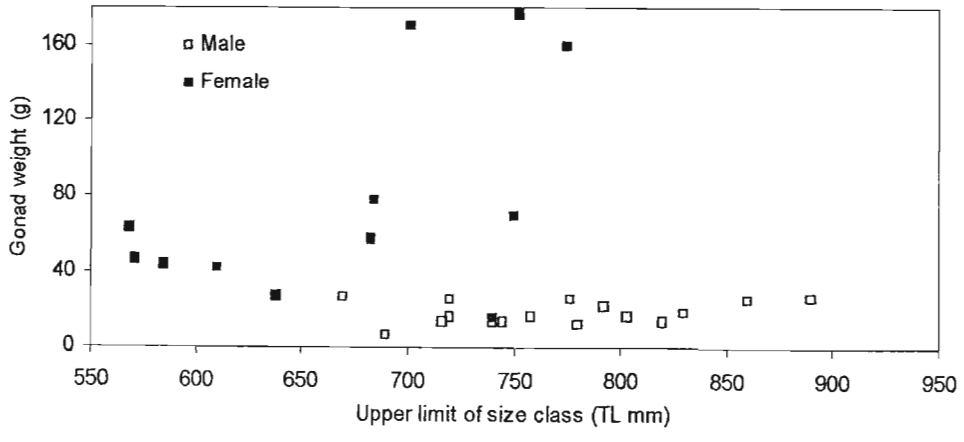


Figure 3.27: Plots of gonad weight for ripe gonads of *E. marginatus* from Mozambique. Data were pooled from May 1995 to March 1996.

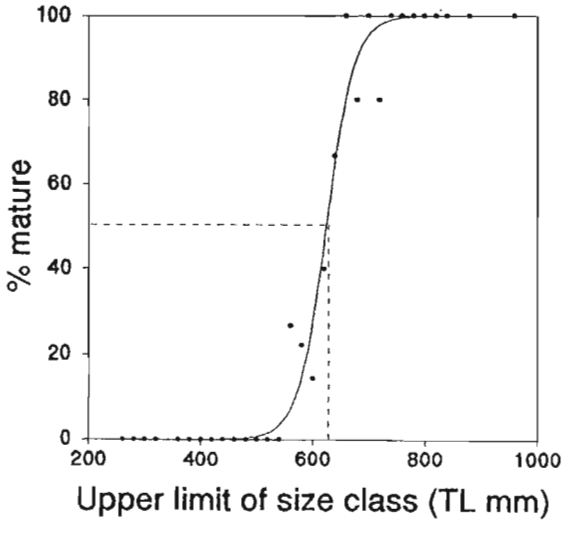
Size at sex change

This was calculated for both southern and northern sampling sites combined, as only four males were obtained from the southern region. The length range between the smallest male (800 mm) and the largest female (950 mm) represents 14% of maximum size. The median value of this range (860 mm) provides an estimate of the size at sex change (Shapiro, 1987). For Mozambique samples, the length range between the smallest male (670 mm) and the largest female (880 mm) represents 22 % of maximum size, and size at sex change is estimated to be 758 mm, which is significantly lower than that in fish from South Africa ($\chi^2 = 20$, $p < 0.001$).

Size at maturity

Minimum lengths at maturity of fish from South African waters, based on the smallest observed mature fish, were 545 mm for females and 800 mm for males. Length at 50% maturity in females was estimated at 624 mm (Figure 3.28), but could not be estimated for males because no immature fish of this sex were obtained. Varying the duration of the spawning season (e.g. by excluding fish from February) resulted in a maximum difference of 4 mm on the estimate of 624 mm. Assuming the spawning season for females in Mozambique waters is from August to March, length at 50% maturity for these fish is estimated to be 580 mm. Minimum sizes at maturity were 560 mm and 670 mm for females and males, respectively.

Figure 3.28: Length at 50 % maturity estimated for female *E. marginatus* from the



northern and southern sampling regions.

Discussion

Despite the absence of fish in the process of sexual transition, there is good evidence to suggest that *E. marginatus* from South African waters is a monandric protogynous hermaphrodite. As in *E. rivulatus*, there is a bimodal size frequency, with males predominating in the larger size classes and having a significantly larger mean size. Males are completely absent from the smaller size classes, with the smallest observed male in the samples from KwaZulu-Natal having a length of 800 mm (TL). The age information presented in chapter 4 also supports the potential for

protogynous hermaphroditism. The youngest age classes comprised immature and mature females only, males were only observed at ages well above the female age at 50% maturity, and the older age classes were almost entirely comprised of males. The youngest observed male was nine years old. Together, this information indicates that males are derived from mature females. Also typical of protogynous populations, the sex ratio for fish from South African waters was significantly skewed in favour of females (5.6 : 1). In Mozambique samples, however, the sex ratio was close to unity, probably because the fish caught in this region were much larger and, hence, included more males. Female-biased sex ratios have also been reported in Tunisia (2 : 1; Bruslé and Bruslé, 1975), in Italy (5 : 1, Spedicato *et al.*, 1995) and in Spain (7 : 1; Zabala *et al.*, 1997a). The latter ratio was based on underwater observations of reproductively active males and females as identified by behaviour and colour patterns.

Histological evidence indicative of protogyny in *E. marginatus* from South African waters includes the occurrence in testes of a membrane-lined lumen and a lamellar structure, both of which indicate a potential previous female phase of development (but see the General Discussion). Mature testes had several sperm sinuses in the gonad walls that contained sperm. Several male gonads contained remnant previtellogenic oocytes, and one also had muscle bundles that may indicate prior spawning as a female. A few precocious cysts of spermatocytes occurred in several female gonads, and one bisexual gonad had equally large proportions of spermatocytes and previtellogenic oocytes. This gonad also had muscle bundles that, in female gonads, were shown to occur shortly after spawning.

Studies by Bruslé and Bruslé (1975; 1976) and Bruslé (1985) have also concluded that *E. marginatus* is a protogynous hermaphrodite. These studies relied heavily on bimodal size frequencies in males and females to infer protogyny, and the existence of gonads with co-occurring male and female tissue was assumed to indicate that these gonads had changed sex. In one publication, though, there was evidence that at least one gonad possessed mature elements of both sexes (Figure 24e in Bruslé, 1985). There has also been a report of artificial induction of female to male sex change in immature *E. marginatus*, using hormones in captive fish (Glamuzina *et al.*, 1998).

Sex change in *E. marginatus* from the Mediterranean was reported as occurring mainly between 700 mm and 900 mm (Bruslé and Bruslé, 1976; Bruslé, 1985), based on the appearance of bisexual gonads in fish in this size range. However, the occurrence of large females (*circa* 1000 mm) and small males (550 mm to 650 mm) suggests that the size at sex change is labile in this area. The estimates of size at sex change using the method of Shapiro (1987) for *E. marginatus* from South Africa and Mozambique, despite being significantly different, both fall within the 700 mm to 900 mm range. Large females were also observed from both these areas, but no males less than 670 mm occurred in samples from either region.

Estimates of size at first maturity in females ranged from 400 mm to 500 mm in France (Chauvét, 1988), to 550 mm to 650 mm in Tunisia (Bruslé, 1985). These were similar to estimates in fish from South Africa (545 mm) and Mozambique (560

mm). As in South African waters, spawning season of western Mediterranean fish occurred in summer (Bouáin and Siau, 1983; Bruslé, 1985).

E. marginatus is distributed mainly on the western and northern coasts of the African continent, as well as on the south-eastern coast (Figure 3.29). In this study, reproductive activity was recorded in both the southern and northern sampling areas in KwaZulu-Natal, and in Mozambique, although the proportion of mature fish in catches was lower in the southern region. It is possible that lower water temperature in this region reduces the incidence of spawning there. Anecdotal reports suggest that there is very limited spawning to the south of KwaZulu-Natal (Dr Malcolm Smale, Port Elizabeth Museum, PO Box 13147, Humewood 6013, South Africa, pers. comm.). Chauvét (1991) reported a lack of spawning at the northern limits of the distribution of *E. marginatus* in the Mediterranean, and attributed this to reduced water temperature. Subsequent work suggests that spawning currently does occur there, possibly as a result of increased water temperatures in the area (Zabala *et al.*, 1997a).

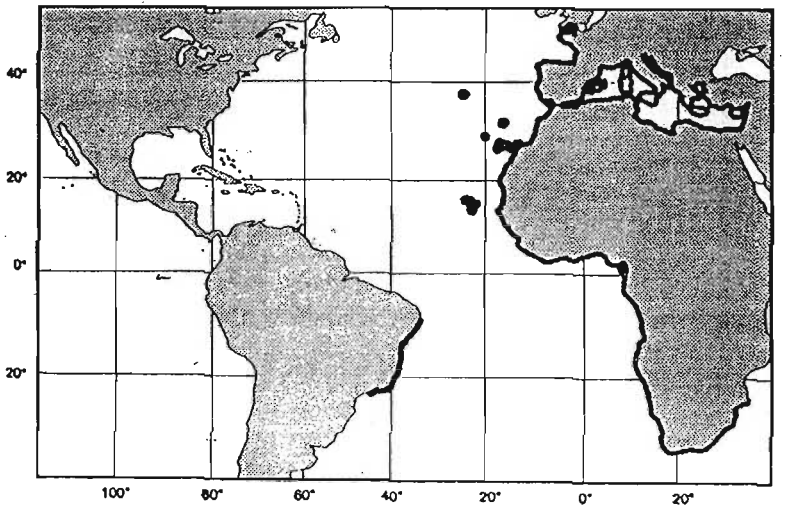


Figure 3.29: Distribution of *E. marginatus* (from Heemstra and Randall, 1993).

Description of gonad stages - E. albomarginatus

Inactive female (n = 292; Figure 3.30a)
This category includes immature fish as well as those fish larger than the size at 50% maturity, and in which there no signs of previous maturity. These gonads contained gonia and closely-packed, previtellogenic oocytes. Virtually all fish sampled (94%) fell into this category, some of which were large. Several (n = 14; 12 % of fish from the northern sampling region) were larger than the minimum size at maturity for fish from this region (600 mm - determined herein), and 10 of these were sampled in the spawning season. Some gonads (n = 7) had a few (< 5) scattered cysts of stage 1 spermatocytes. In the Mozambican samples, inactive female gonads (n = 11) also occurred in large fish. Of these, nine fish were larger than the size at 50% maturity for this region (341 mm) and five were sampled during the spawning season. It was not possible to determine whether these inactive fish would matured later or whether they had already matured and then regressed to this inactive state. One gonad had a few (< 5) cysts of stage 1 spermatocytes.

Mature, resting female (Figure 3.30b)
No mature, resting female gonads were obtained in fish from KwaZulu-Natal waters. In gonads collected from fish from Mozambique (n = 18), previtellogenic and cortical alveolar oocytes were present. Several gonads exhibited signs of prior spawning in the form of prominent muscle bundles that appeared after the spawning season (Figure 3.30.1). One gonad had a few (< 5) cysts of spermatocytes.

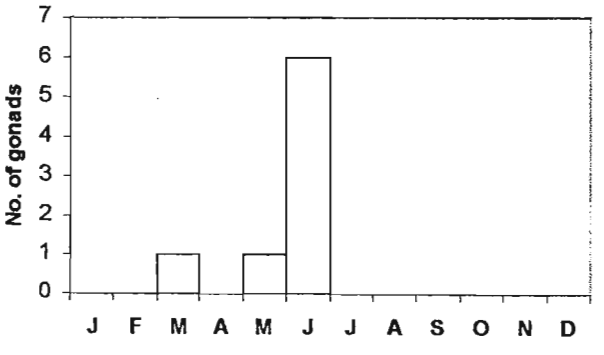


Figure 3.30.1: Monthly occurrence of mature, resting, female *E. albomarginatus* gonads with muscle bundles. Mozambique samples only; monthly data from May 1995 to September 1997 were pooled.

Mature, ripe female (n = 5; Figure 3.30c)
Gonads of this stage were only obtained from the northern sampling region and from Mozambique. Ovaries were substantially larger than those in a resting stage, and contained previtellogenic and cortical alveolar oocytes, as well as many vitellogenic oocytes. A total of 53 of these gonads were obtained from Mozambique, and hydrated eggs were recorded in these gonads in February and October.

Post-spawning female (Figure 3.30d)
No post-spawning female gonads were obtained in fish from South African waters. In gonads of this stage collected from fish from Mozambique (n = 3), there was widespread atresia of vitellogenic oocytes. Cytoplasmic strands were extensive and previtellogenic oocytes were numerous.

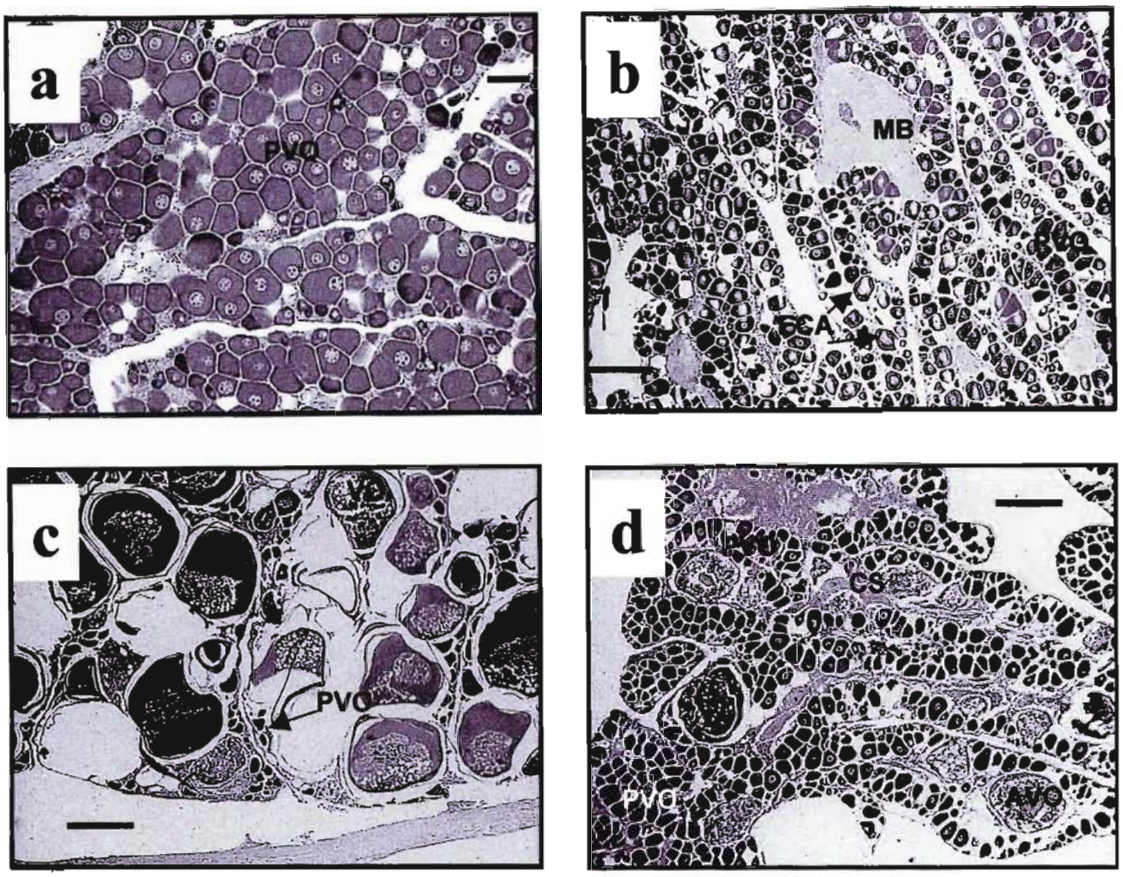


Figure 3.30: Cross-sections of female *E. albomarginatus* gonads.

a Immature, female gonad, with previtellogenic oocytes (PVO). TL 580 mm, January 1995. Scale bar = 100μ.

b Mature, resting, female gonad, showing previtellogenic oocytes (PVO), early cortical alveolar oocytes (ECA) and muscle bundles (MB). TL 620 mm, June 1995. Scale bar = 300μ.

c Ripe female gonad showing previtellogenic oocytes (PVO), vitellogenic oocytes (VO) and early hydrated eggs (HE). TL 600 mm, February 1995. Scale bar = 300μ.

d Post-spawning, female gonad showing atretic, vitellogenic oocytes (AVO), previtellogenic oocytes (PVO), and cytoplasmic strands (CS). TL 570 mm, March 1995. Scale bar = 300μ.

Inactive bisexual (n = 5; Figure 3.31a,b)
These gonads largely consisted of previtellogenic oocytes, with between 30 and 50 cysts of stage 1 and/or 2 spermatocytes. In two of these gonads, there was a small cluster of cysts and gonia adjacent to the dorsal blood vessel (similar to the situation in inactive, bisexual *E. andersoni*), as well as scattered cysts throughout the lamellae. In two other gonads, the cysts were scattered throughout the gonad, while in one gonad, the cysts were mainly located on the periphery of the gonad. In the Mozambican samples, there were three gonads of this stage. One of these had several muscle bundles, which suggests prior female functioning. There were also numerous large melano-macrophages in this gonad.

Mature, resting male (n = 6; Figure 3.31c)
Most of the gonad consisted of spermatogonia and stage 1 and 2 spermatocytes, with occasional cysts of sperm either in the sperm sinuses or in a few of the lobules. No male gonads were recorded in samples from the southern sampling region. In the Mozambican samples, there were 10 mature, resting male gonads. Two of these contained previtellogenic oocytes that were fairly numerous. Large melano-macrophages occurred in all male gonads.

Mature, ripe male (n = 2; Figure 3.31d)
Stage 1 and 2 spermatocytes occurred, but the gonads were dominated by later stages of spermatogenesis. Sperm were present in both the lobules and the sperm sinuses. In some, the lobule walls had split and large areas of sperm were evident. In samples of Mozambican fish, 11 gonads of this stage were recorded.

Length frequencies and sex ratios

Length frequency histograms of the various sex and maturity stages (Figure 3.32) showed that inactive female fish predominated in samples from KwaZulu-Natal waters, despite the fact that a substantial proportion of samples were obtained during the months of October to February when spawning was likely to occur (Table 3.2). Mozambican samples were dominated by mature fish that occurred in almost all size classes. Males were restricted to the larger size classes in both Mozambican and KwaZulu-Natal samples.

Statistical comparisons of lengths and sex ratios of mature fish were not undertaken for samples from KwaZulu-Natal waters because numbers were low. Mature males ranged in length from 511 mm to 820 mm, females from 600 mm to 810 mm. Of the samples from Mozambican waters, mature males ranged in length from 591 mm to 840 mm, females from 329 mm to 810 mm, and their mean sizes (746 mm and 569 mm, respectively) were significantly different ($t = 7.3$, $DF = 95$, $p < 0.001$). There were significantly fewer mature males than mature females (0.31 : 1, $n = 97$, $\chi^2 = 35.8$, $p < 0.001$).

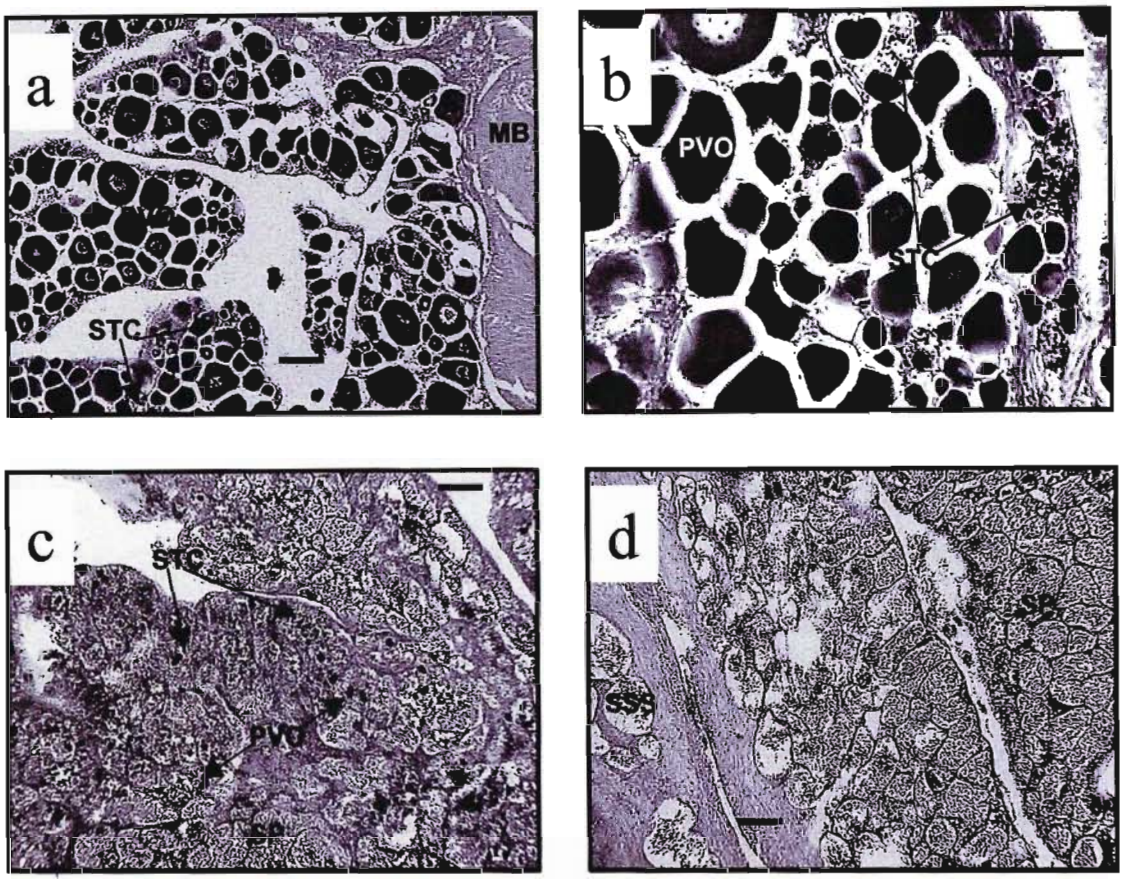


Figure 3.31: Cross-sections of *E. albomarginatus* gonads.

a Inactive, bisexual gonad, with previtellogenic oocytes (PVO), muscle bundles (MB) and scattered cysts of spermatocytes (STC). TL 790 mm, July 1995. Scale bar = 100μ.

b Magnified view of (a), with previtellogenic oocytes (PVO) and scattered cysts of spermatocytes (STC). Scale bar = 100μ.

c Resting, male gonad, with scattered previtellogenic oocytes (PVO), cysts of spermatocytes (STC) and cysts of sperm (SP). TL 727 mm, August 1995. Scale bar = 100μ.

d Ripe, male gonad, showing sperm (SP) in the lobules and in a sperm sinus (SSS). TL 745 mm, March 1995. Scale bar = 100μ.

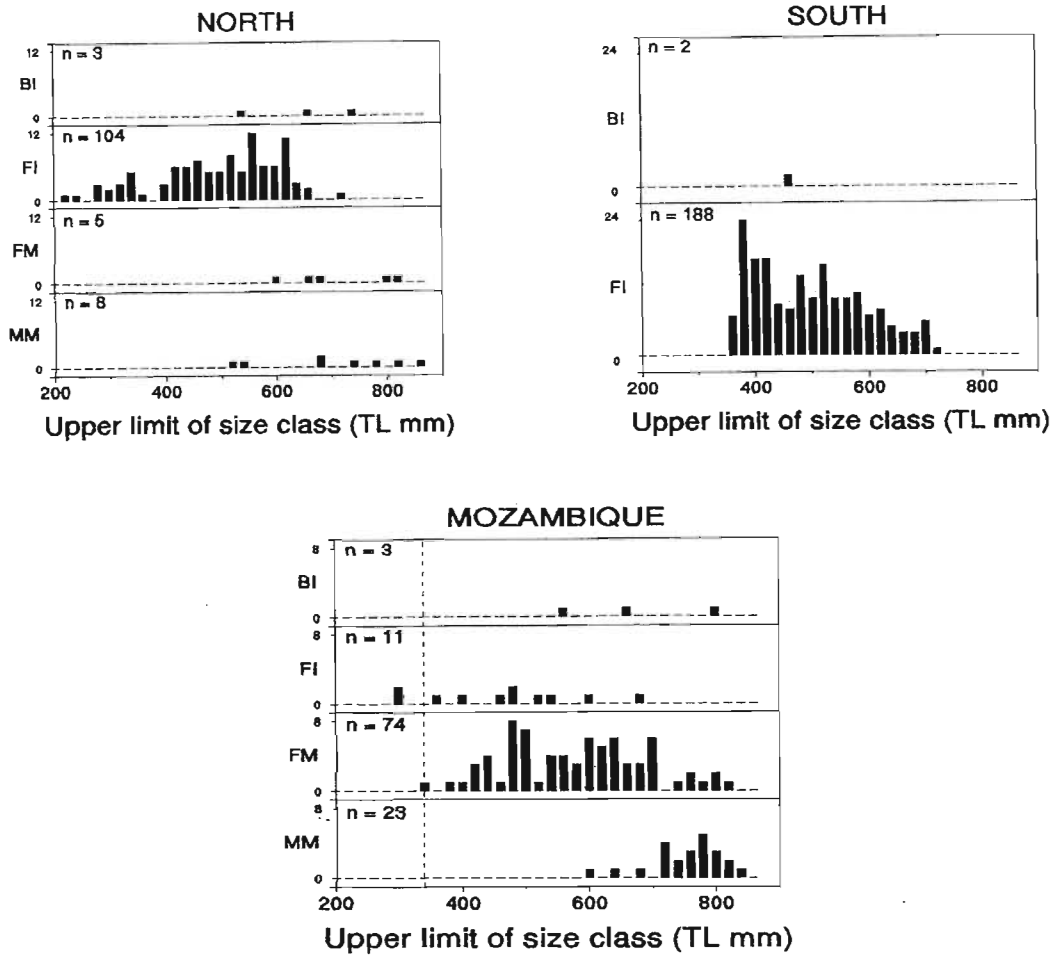


Figure 3.32: Length frequencies (by number) of *E. albomarginatus* from northern and southern sampling areas in KwaZulu-Natal, and Mozambique. BI = inactive bisexual, FI = inactive female, FM = mature female, MM = mature male. The dashed line indicates size at 50% maturity in females from Mozambique.

Spawning season

Low numbers of mature fish precluded the use of a gonad index to determine spawning season in South African waters. A plot of the proportions of each observed gonad stage on a monthly basis indicated that female spawning season appeared to be extended, with spawning potentially occurring from October to February (Figure 3.33). Histologically, ripe males were observed in December.

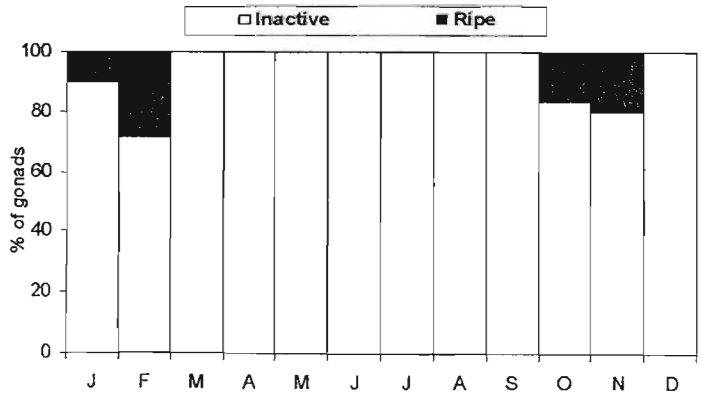


Figure 3.33: Relative monthly percentages of female *E. albomarginatus* gonad stages from the northern sampling area. Monthly data from May 1995 to September 1997 were pooled (n = 109).

Based on the gonad index (Figure 3.34) and the proportions of gonad stages per month (Figure 3.35), spawning in Mozambican waters appeared to occur from October to March, although data were incomplete. Ripe females occurred from October to March, and ripe males occurred in October and from December to March. The size of ripe ovaries was mostly greater than that of testes (Figure 3.36).

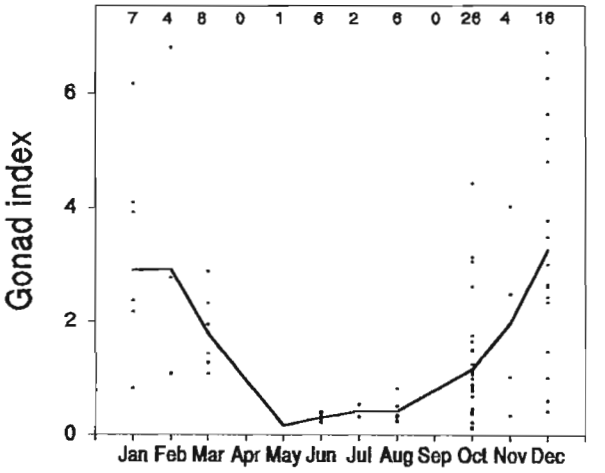


Figure 3.34: Monthly gonad indices for female *E. albomarginatus* from Mozambique. The line joins the monthly means. Monthly data were pooled from May 1995 to March 1996. Monthly sample sizes are shown on the top of the graph.

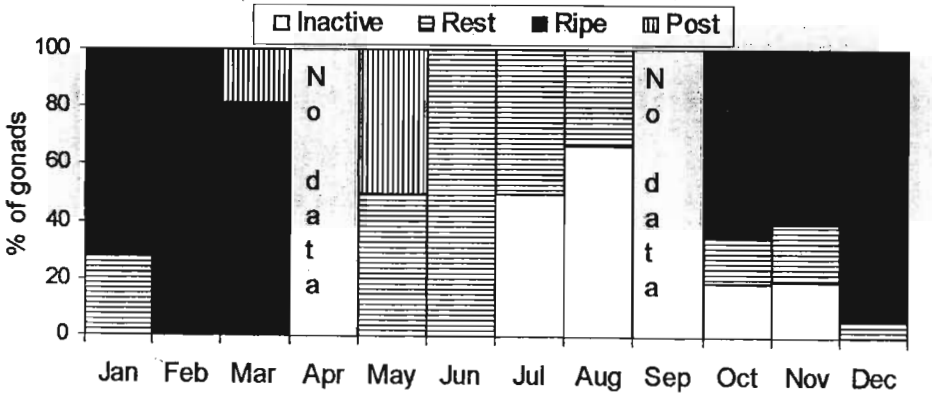


Figure 3.35: Relative monthly proportions of gonad stages for female *E. albomarginatus* from Mozambique. Monthly data were pooled from May 1995 to March 1996 (n = 85).

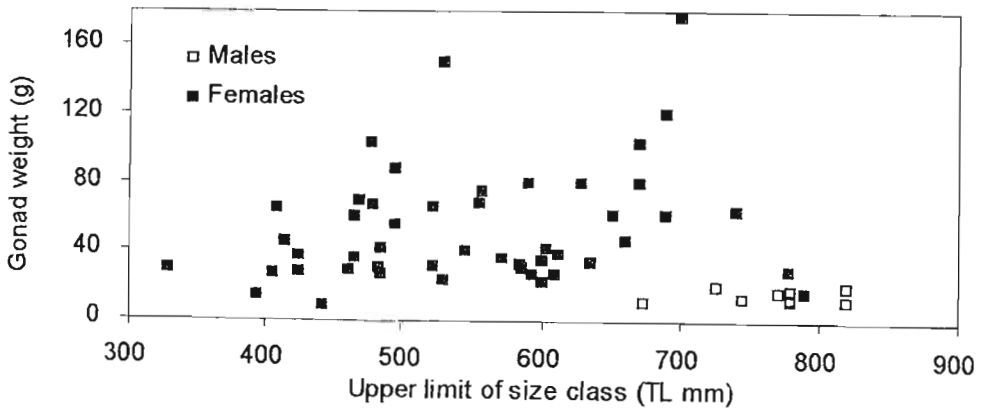


Figure 3.36: Plots of gonad weight for *E. albomarginatus* from Mozambique, during the spawning months (October 1995 to March 1996).

Size at sex change

For fish from South African waters, this was only calculated for the northern sampling region, because no males were obtained from the southern region. The length range between the smallest male (511 mm) and the largest female (810 mm) represented 35 % of maximum size. The median value of this range (665 mm) provides an estimate of the size at sex change (Shapiro, 1987). For Mozambique samples, the length range between the smallest male (591 mm) and the largest female (810 mm) represented 26 % of maximum size. Size at sex change was estimated to be 695 mm, which was not significantly different from that in fish from South Africa ($\chi^2 = 0.44$, $p = 0.05$), although the number of samples from the latter area is low.

Size at maturity

Minimum lengths at maturity of fish from South African waters, based on the smallest observed mature fish, were 600 mm for females and 511 mm for males. Length at 50% maturity was not estimated for these fish because very few mature fish were obtained. Assuming the spawning season in Mozambique waters is from October to March, length at 50% maturity for females was estimated to be 341 mm (Figure 3.37). Minimum sizes at maturity of fish were 329 mm and 591 mm for females and males respectively, considerably different from KwaZulu-Natal.

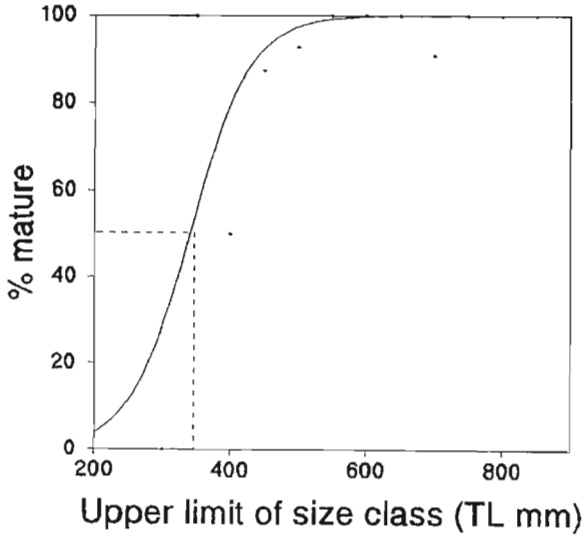


Figure 3.37: Length at 50% maturity for female *E. albomarginatus* from Mozambique.

Discussion

Based on the findings presented here, there is some evidence to suggest that *E. albomarginatus* is a monandric protogynous hermaphrodite. In the Mozambican samples, there was a bimodal size frequency, with males predominating in the larger size classes and having a significantly larger mean size. No small males were observed. Also typical of protogynous populations, the sex ratio of the Mozambican samples was significantly skewed in favour of females. Too few mature fish from

KwaZulu-Natal waters were obtained to warrant detailed interpretation, although males were also restricted to the larger size classes. However, age information for these fish also supports the potential for protogynous hermaphroditism (Chapter 4). The youngest age classes comprised females only, the youngest male was older than the youngest mature female, and the older age classes were largely comprised of males. The youngest observed male was seven years old. Together, this information indicates that males are derived from mature females.

Histological evidence includes the occurrence in testes of a membrane-lined lumen and a lamellar structure, both of which indicate a potential previous female phase of development (but see General Discussion). Mature testes had several sperm sinuses in the gonad walls that contained sperm i.e. there was no clearly identifiable sperm duct as found in gonochorists. Remnant previtellogenic oocytes occurred in a few male gonads, and a few precocious cysts of spermatocytes occurred in some female gonads. Several gonads contained inactive female tissue (previtellogenic oocytes) together with what appeared to be proliferating male tissue in the form of numerous cysts of spermatocytes. One of these gonads also had muscle bundles that, in other gonads, were shown to occur shortly after spawning as a female. This gonad could be in the process of transition from female to male.

Of the four serranids investigated in this study, *E. albomarginatus* has the most limited distribution (Figure 3.38). No mature fish were recorded in samples from the southern sampling region, and very few were obtained from the northern region. It is therefore not possible to estimate size at maturity in female fish from South African waters, although it is clear that it is substantially smaller in fish from Mozambique. Presumably environmental conditions are less suitable for spawning in South African waters, and lower water temperature at these higher latitudes appears to be the reason. However, there are several large fish in Mozambican samples that showed no sign of reproductive activity during the spawning season. As in *E. andersoni*, it is possible that these fish either mature only at a large size, or they had already matured and had rapidly regressed to an inactive state.

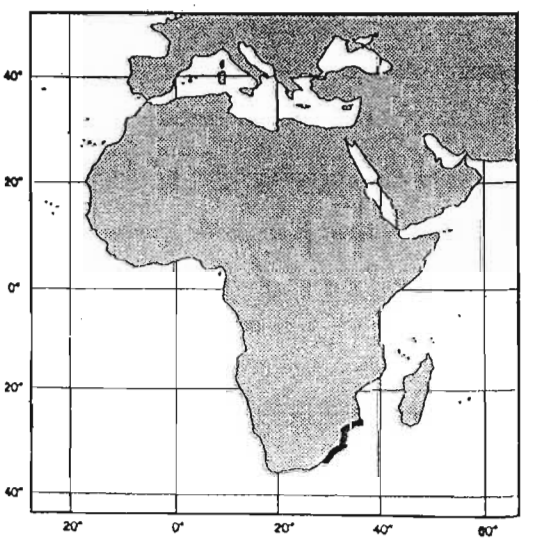


Figure 3.38: Distribution of *E. albomarginatus* (from Heemstra and Randall, 1993).

General discussion

Based on the appearance of ripe gonads in several months of the year, all four rockcods investigated in this study have extended spawning seasons of about four to five months. Three species, *E. andersoni*, *E. marginatus* and *E. albomarginatus*, spawn in spring and summer months, while *E. rivulatus* spawns in winter and spring. Within the spawning season, peaks in gonad indices suggest months in which spawning activity may be concentrated. This concurs with the review by Shapiro (1987), who noted similar patterns in other serranids. It should be noted that in this study, the duration of spawning season was inferred from the relative sizes of ovaries, and the relative proportions of vitellogenic oocytes and sperm in ovaries and testes respectively. Hydrated eggs and/or post-ovulatory follicles, which allow for more precise determination of spawning season, were only noted in some months of the proposed spawning seasons in all four species. More extensive sampling and histology of ripe gonads could therefore provide greater clarity on the seasonality of spawning.

The co-occurrence of post-ovulatory follicles and hydrated eggs in a few *E. andersoni* and *E. rivulatus* gonads suggests that these species are capable of spawning more than once within the spawning season. Mackie (2000) used similar information to conclude that *E. rivulatus* in Western Australia could spawn more than once within a two or three day period. He also observed that this species spawned within a short period of about six days, followed by a non-spawning period during which the next batch of eggs ripened. Co-occurrence of vitellogenic oocytes and hydrated eggs or post-ovulatory follicles was noted in all four species investigated herein, which also suggests that batches of eggs would be released on more than one occasion. This is speculative, though, and would need to be validated by sampling of ripe ovaries at short time intervals in order to follow the modal progression of oocyte diameters through the spawning season. The sampling procedure employed in this study precluded such an approach.

In all four species, ripe ovaries were considerably larger than ripe testes. Equal-sized ripe gonads in males and females is suggestive of group spawning, when multiple males mate with a single female under conditions of intense sperm competition (Choat and Robertson, 1975; Robertson and Warner, 1978). In contrast, sperm competition is reduced in pair-spawning, and the male need not make a major investment in gamete production, hence the testis size is small relative to the ovary. Spawning of the serranid species investigated here is therefore likely to occur in pairs, or in small groups with a single male and multiple females, as has been observed in *E. marginatus* in Spain (Zabala *et al.*, 1997b) and in *E. rivulatus* in Australia (Mackie, 2000). In support of this, anecdotal reports from spearfishers suggest that *E. andersoni*, *E. rivulatus* and *E. marginatus* generally occur in small groups of less than 10 individuals. Only on one occasion has a large (*circa* 100 individuals) group of *E. andersoni* been observed (B. Leisegang, Natal Underwater Union, pers. comm.), although this was outside the spawning season, and occurred on the southern coast of KwaZulu-Natal, where almost no spawning occurs in this species. However, these observations were restricted to water depths less than 30 m.

Substantial increases in catches of a species during the spawning season suggests that seasonal aggregation occurs. Perusal of monthly catch returns by commercial skippers, and plots of monthly catch per unit effort showed that catch rates of serranids in the northern sampling area increased during the summer months (Figure 3.39), when three of the four species investigated in this study were found to spawn. Unfortunately, non-identification of serranids to species level in catches may be confounding interpretation of this seasonal trend, although the majority of the serranid catch in the northern area was found to consist of *E. andersoni*. Also, the multispecies nature of the fishery implies that fishing effort is not directed solely at serranids, which also complicates interpretation. The information obtained from skipper interviews was inconclusive in this regard. Of interest were unusually large catches of *E. andersoni* that were either observed (one occasion) or heard of (two occasions). Two of these catches were made in the spawning season, and one was made shortly thereafter. Only the latter catch was sampled, and this consisted of equivalent numbers of inactive/resting fish and ripe/post-spawning fish. Most of the mature fish were ripe (42%) or post-spawning (34%) males. However, there is insufficient evidence from these catches to conclude that *E. andersoni* aggregate in order to spawn.

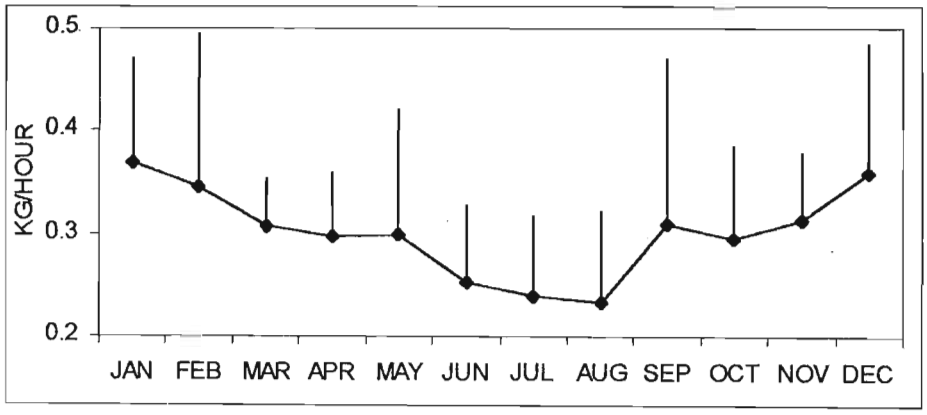


Figure 3.39: Plot of mean monthly catch rates (plus one SD) of serranids (all species combined) based on commercial catch returns for the northern sampling area of KwaZulu-Natal (1986-1998).

There are few studies on the formation of spawning aggregations in any of the four species of serranids investigated here. Zabala *et al.* (1997a, 1997b) report a more than 10-fold increase in numbers of *E. marginatus* in the spawning season, which qualifies as a spawning aggregation using the definition of Domeier and Colin (1997). *E. rivulatus* in Western Australia, however, did not appear to aggregate to spawn (Mackie, 1998). More intensive sampling of catches throughout the year could elucidate spawning aggregation tendencies in South African serranids. This would require co-operation from fishers to obtain greater resolution on catch localities. However, the best evidence is observation of aggregations in the act of spawning (Domeier and Colin, 1997).

In all four species, there were females larger than the size at 50% maturity that showed no signs of reproductive activity during the spawning season. This was particularly marked in the case of *E. andersoni* and *E. albomarginatus*. In the former species, almost no spawning was recorded in the southern sampling region, while in

the latter species, very few mature fish were recorded in KwaZulu-Natal samples i.e. spawning appeared to occur almost exclusively in Mozambican waters. Even in Mozambican samples, though, large, inactive females were not uncommon during the spawning season. As described in the discussions for the individual species, it was impossible to resolve whether such fish first mature at a large size, or if they had already matured and then rapidly regressed to an inactive state. Also possible is that these are mature fish that did not spawn every year, and precedents for this were discussed. Another possibility that was discussed was that environmental conditions were not always suitable for spawning, which could account for between-area differences in spawning activity, but does not explain the within-area lack of spawning activity in some large fish. An alternative explanation for non-spawning in mature fish each year may be that long-lived species such as these are under selection to maximise reproductive fitness over their lifetime. This may be achieved by accepting interannual variability in reproductive success, in contrast to short-lived species that must maximise reproduction each year (Henderson and Seaby, 1999).

For some of these fish, then, maturity may be delayed until social, physiological and/or environmental conditions are suitable. For large, inactive *E. andersoni* in the southern sampling region, and the mostly inactive *E. albomarginatus* in South African waters, the question arises as to whether these fish ever spawn. If the environment is limiting, then it is possible that these fish could migrate to suitable spawning grounds. Limited tagging data for *E. andersoni* suggests that this is not the case. Of the recaptured fish originally tagged south of Durban, none have shown south to north movement of any significance (Appendix 2). Furthermore, it may be anticipated that, if there is a northward movement by mature-sized fish in order to spawn, then the mean length of the southern population would be smaller than the northern one. This assumes that, in both regions, the effects of fishing on mean length are similar, and that there are no environmental constraints to growth. In the case of *E. andersoni*, the mean lengths of northern and southern fish were not significantly different ($t = 1.92$, $DF = 837$, $p = 0.06$). There was also no significant difference between the mean size of *E. andersoni* from the southern region before and during the spawning season ($t = 1.15$, $DF = 402$, $p = 0.25$), which also suggests that there was no extensive movement of larger fish prior to the spawning season. This last comparison will not be affected by disparities in north/south fishing effects, but could be affected by seasonal differences in fishing effects, if these exist. For *E. albomarginatus*, though, fish from the southern population were significantly smaller than their northern counterparts ($t = 5.8$, $DF = 319$, $p < 0.001$), hence there may be south to north movement of larger individuals of this species.

The age information for these species (Chapter 4) is, however, of interest. No *E. andersoni* older than six years were recorded in the southern sampling area, while, for *E. albomarginatus*, the oldest fish in this area was eight years old. This suggests that there may be migration of older fish towards the north, where spawning of these species occurs. These observations are perhaps circumstantial, and an intensive tagging programme would assist in determining whether fish spawn in the south. This lack of reproductive activity towards the southern limit of their range has been reported for other endemic, subtropical, South African fishes that are resident in the same area as *E. andersoni* and *E. albomarginatus* e.g. the sparids *Chrysoblephus puniceus* (Garratt, 1985) and *C. anglicus* (Garratt *et al.*, 1994).

All four species examined here show evidence of protogynous hermaphroditism. In *E. andersoni*, the reproductive style is diandric protogynous hermaphroditism, while in *E. rivulatus*, *E. marginatus* and *E. albomarginatus* it is monandric protogynous hermaphroditism. To date, only one other epinepheline serranid, *E. striatus* from the tropical western Atlantic, has shown evidence of juvenile female to male development. This species was classified as a gonochorist, as there was no evidence of mature female to male sex change (Sadovy and Colin, 1995). All epinephelids examined in other studies have proved to be monandric protogynous hermaphrodites, although the evidence is not always strong. *E. andersoni* shares similar characteristics with *E. striatus*, in that both species exhibit overlapping mature male and female size frequencies, similar mean sizes of males and females, and a sex ratio of mature fishes close to unity. The latter species, however, spawns in extremely large aggregations, and has ripe male and female gonads that are equivalent in size, consistent with group-spawning (Sadovy and Colin, 1995). In contrast, there is a substantial difference in ripe gonad size between males and females in *E. andersoni*, which indicates that this species may spawn in pairs or in small groups consisting of one male and several females. The sexual pattern of this species, diandric protogynous hermaphroditism, therefore differs from other epinepheline serranids described to date. Other serranid taxa, however, also show deviation from the typical monandric pattern, such as members of the genera *Paralabrax* (Smith and Young, 1966; Hastings, 1989) and *Cephalopholis* (Siau, 1994). Diandry is more commonly associated with the families Labridae and Scaridae in which there is sexual dimorphism and a combination of group and pair spawning (e.g. Robertson and Warner, 1978; Warner and Robertson, 1978). Neither of these characteristics is evident for *E. andersoni*.

The occurrence of scattered, isolated cysts of spermatocytes in female gonads is typical of the infiltration of male tissue in gonads of other protogynous epinepheline serranids e.g. *E. morio* (Moe, 1969), *E. guttatus* (Shapiro *et al.*, 1993b) and *E. striatus* (Sadovy and Colin, 1995). The configuration of the gonads of *E. rivulatus*, *E. marginatus* and *E. albomarginatus* is undelimited, with male and female tissue not separated by connective tissue, but intermixed. Again, this is characteristic of epinepheline serranids (Smith, 1965). Typically, the transition process commences with the appearance of a few, scattered, isolated cysts of spermatocytes that proliferate until the gonad is essentially male in appearance. The appearance of small numbers of these cysts in several ovaries either signifies that the transitional process has been initiated in these fish, or at least that they are capable of changing sex if the appropriate cues are received. In *E. andersoni*, though, the configuration of the male tissue as it infiltrates the gonad is considerably different from the typical epinepheline situation. This has been described in detail in the description of the gonads for this species. Thus, the male tissue, although not physically separated from the female tissue, is spatially well-defined, particularly in the early stages of ontogeny.

There is difficulty in determining the sexual pattern of groups such as the serranids that have probably evolved from a protogynous ancestor (Smith, 1959; Smith, 1967). In these fishes, the ancestry has resulted in an early female-like phase from which males can develop directly. Thus, the ovarian appearance of the gonad i.e. a lumen and lamellae, does not prove earlier female function, but reflects the

ancestry. Smith and Young (1966) discussed this in a paper on *Paralabrax clathratus* from California, describing male testes that had an ovarian lumen and lamellae, but with no evidence for sex change. Thus, the earlier use of a female-like appearance of the gonad as a criterion for hermaphroditism (Sadovy and Shapiro, 1987), may not be appropriate (Professor Yvonne Sadovy, University of Hong Kong, Pok Fu Lam Road, Hong Kong, pers. comm.).

In their review of sexual transition, Sadovy and Shapiro (1987) reported that the duration of transition in other protogynous species varies from a few days to several months, although no epinepheline serranids were included in their list. The low numbers of transitional gonads recorded in all four species investigated in this study could indicate that the duration is short, or that only a few fish change sex, or that sampling was inadequate (Sadovy and Shapiro, 1987). However, a low incidence of transitionals appears to be typical of epinepheline serranids (Shapiro, 1987), perhaps in part because sex change occurs rapidly. In fact, Mackie (1998) reported that *E. rivulatus* could change sex in as little as three weeks.

Variability in size/age of transition in turn suggests that the process is behaviourally induced (Shapiro, 1984; Shapiro, 1987; Ross, 1990), rather than occurring at an evolutionarily pre-determined size as initially suggested by Ghiselin (1969) and Warner (1975). The latter author subsequently acknowledged that examples of purely genetic determination of sex change are probably rare (Warner, 1988). In this study, sex change occurred over a wide size range in all four species, and there was some geographic variation in size at transition for *E. rivulatus*, *E. marginatus* and *E. albomarginatus*. Furthermore, the occurrence of large females in all four species suggests no predisposition to change sex at a particular size (assuming that all individuals possess the ability to change).

Simplistically stated, current sex change theory for protogyny suggests that an individual female "chooses" whether or not to change sex by assessing the current sex ratio in the population, or by assessing the ratio of dominance : submissive encounters she experiences (Shapiro, 1988). So, if there are only a few males, a large female may change sex and become male. If the female experiences a large number of interactions with small, submissive females, she may also choose to change sex. In all cases, the decision to change sex is based on the premise that future chances of producing progeny will be improved (Charnov, 1982). In the case of protogyny, for example, larger males could enjoy a disproportionate advantage during spawning because of their ability to defend a spawning territory against other males and attract many females (Warner, 1975).

In species that aggregate to spawn, but are dispersed for the remainder of the year, the aggregation period is the logical time for individuals to make decisions on their future reproductive potential while functioning as their current sex (Shapiro *et al.*, 1993a). Appearance of transitional individuals after the spawning season or between spawning seasons would thus support the theory that the process is initiated during the spawning season (Shapiro *et al.*, 1993a). The scarcity of transitionals observed in this study makes it difficult to establish the timing of the transitional period with certainty, since there are few examples to examine, particularly in *E. marginatus* and *E. albomarginatus*. Transitional individuals of *E.*

andersoni were recorded both outside and during the spawning season, which suggests that transition is not initiated during a narrow time period. This in turn argues that *E. andersoni* does not aggregate to spawn during a limited period, and that decisions to change sex can be made over a period of several months. This species is diandric, though, and hence is not a good example to examine the temporal nature of sex-change initiation.

In contrast, *E. rivulatus* in Western Australian waters lives in small groups throughout the year, with no apparent aggregation for spawning (Mackie, 1998). This enables decisions on sex change to be made at any time, because there would be continual cueing as to whether to change sex or not. Under these circumstances, transition could be expected to take place throughout the year. However, in both this and the Australian study, transitional individuals were only found in a few months shortly after the spawning season. The number of transitionals observed in both of these studies is low, however. Sex change in this species is reported to occur in as little as three weeks (Mackie, 1998), so it is possible that few transitional individuals were sampled because they exist for such a limited amount of time.

In concluding this discussion, it needs to be emphasized that samples were mostly collected from commercial or recreational catches, which excluded a large part of the populations of all four species. For each sampling region, it is unknown whether the samples were obtained from one or more sub-communities, which could therefore have biased the population structure (Sadovy and Shapiro, 1987). Ideally, a single community should be examined over its full size range, and at regular intervals. This ideal could not be attained for the species investigated here. Nevertheless, the information obtained advances our knowledge of hermaphroditism and, in the case of *E. andersoni*, supports the prediction of Smith (1965) that additional reproductive patterns within the serranids would be discovered.

CHAPTER 4: AGE, GROWTH AND MORTALITY

Introduction

Information on the ages and lengths of fish enables the determination of their growth rate and longevity, factors that, in part, suggest the rate at which a population can be harvested. In species with fast growth rates, populations replace themselves quicker than species with slower growth rates: the faster-growing species mature quicker, reproduce earlier and die earlier. Faster-growing fishes can therefore withstand greater harvesting pressure than slow-growing fishes. Information on the ages of fish also helps in the elucidation of sexual pattern: for example, the exclusive appearance of males in the oldest age classes of a species will, together with histological information, provide strong evidence for protogynous hermaphroditism (Sadovy and Shapiro, 1987).

Age and growth information is generally obtained via one or more of the following three methods: by counting periodically formed marks on hard structures such as scales or bones; by measuring growth in individual fish over time, e.g. using mark and recapture; or by measuring the change in modal length of a population over time (Manooch, 1982). All three methods have strengths and weaknesses, but the most popular approach used in ageing of long-lived reef fish species is via by counting annual rings in sagittal otoliths (Hecht and Smale, 1986). The advantages of this approach are that large numbers of samples are not required, and that ages of individual fish can be established, which is useful for intraspecific comparisons of variation in growth (Manooch, 1987). It does, however, require that the fish are killed in order to obtain the otoliths.

A review of literature on the ageing of serranids revealed that age determination by means of otoliths has been undertaken for a large number of species, and from a range of localities e.g. *Centropristis striata* from the Gulf of Mexico (Hood *et al.*, 1994), *Plectropomus leopardus* from northern Australia (Ferreira and Russ, 1994), *Paralabrax clathratus* from the north-eastern Pacific (Cordes and Allen, 1997), *Epinephelus quernus* from Hawaii (Williams and Lowe, 1997), *Cephalopholis panamensis* and *E. labriformis* from the eastern Pacific (Craig *et al.*, 1999), *Mycteroperca microlepis* from the Gulf of Mexico (Harris and Collins, 2000), *E. malabaricus* and *E. coioides* from northern Australia (Sheaves, 1995) and *E. marginatus* from the Mediterranean (Bouchereau *et al.*, 1999). Although no ageing studies have been undertaken on serranids in southern Africa waters, several studies on reef-associated sparid fishes in the region have successfully utilised otoliths to determine growth of these species e.g. Buxton and Clarke (1986), Smale and Punt (1991), Buxton (1993), Garratt *et al.* (1993), Mann and Buxton (1997), Chale-Matsau *et al.* (2000). Consequently, age determination from otoliths was the method chosen in this study.

Having obtained a range of age estimates and their associated lengths, a growth curve or model can be fitted to the data, parameter estimates of which summarise the growth characteristics of the species being investigated. There are a variety of growth models, the shapes of which reflect the growth process e.g. Pütter, von Bertalanffy, Richards, Gompertz, logistic, exponential and linear (Ricker, 1979), and

Schnute (1981) describes the dilemma faced by those who wish to fit a model to age at length data. Apart from the exponential and linear models, these models characteristically incorporate two key parameters: $L\infty$, the asymptotic mean length which the fish would attain if they grew indefinitely and k, the Brody growth coefficient reflecting the rate at which $L\infty$ is attained. The von Bertalanffy model is traditionally used to describe growth in fish, although Ricker (1979), Schnute (1981) and Moreau (1987) have demonstrated that there is a close relationship between all the asymptotic growth models. Pauly (1981), however, demonstrated the biological basis to the von Bertalanffy model and described two versions:

$$L(t) = L\infty\left(1 - e^{-k(t-t_0)}\right) \qquad L(t) = L\infty\left(1 - e^{-kD(t-t_0)1/D}\right)$$

(Special von Bertalanffy) (General von Bertalanffy)

where: $L(t)$ = mean length at time t
$L\infty$ = asymptotic length
k = growth coefficient
t_0 = theoretical age at zero length
D = a factor which, when growth in weight is isometric, has a value of 1, resulting in the special von Bertalanffy equation (Pauly, 1984)

The special von Bertalanffy model has been traditionally used to describe fish growth, although Pauly (1984) noted that this version of the model is only biologically justifiable when describing growth of very small (<1 g) fish.

In view of the above, a broad approach was taken to the fitting of growth models to the age-length data, rather than being predisposed to fitting a particular model. This chapter therefore describes the age determination process and the fitting of appropriate growth models in four species of South African serranids. Growth parameter estimates, together with estimates of natural mortality and fishing mortality, will be used in the following chapter to undertake stock assessments of these four species.

Materials and methods

Age estimation

During the course of sampling to collect gonads of *E. andersoni*, *E. rivulatus*, *E. marginatus* and *E. albomarginatus* in KwaZulu-Natal (Chapter 3), the sagittal otoliths of a subsample of fishes were also removed and total lengths (mm) of fish were collected over the size range of fishes caught by the skiboat fishery. Otoliths were cleaned and stored dry in envelopes until processing. An attempt was made to obtain 20 pairs of otoliths per 50 mm length class for *E. andersoni*, *E. marginatus*, and *E. albomarginatus*, and in 25 mm length classes for *E. rivulatus*. Otoliths from small and/or sub-legal-sized fishes (< 400 mm TL in the case of *E. andersoni*, *E. marginatus* and *E. albomarginatus*) were collected by research fishing or spearing in the Durban region, and from illegal catches confiscated by the KwaZulu-Natal Nature Conservation Service.

The otoliths of all four species were fairly thick and opaque, and, despite the testing of several methods, attempts at obtaining age estimates from whole otoliths were unsuccessful. Methods tested included suspending otoliths in glycerine and viewing against a dark background using reflected light and a dissecting microscope; suspending otoliths in water and observation using transmitted light; and heating the otoliths in an attempt to improve readability. Subsequently, one of each pair of otoliths was chosen randomly, and embedded in clear casting resin in a semi-circular PVC tube mould. Several transverse sections (0.6 – 0.8 mm thick) were made through the central region of each otolith using a single diamond-coated blade. Transverse sections, as opposed to longitudinal sections, were used, as the former provided the clearest presentation of growth zones. For age estimation, the sections were placed in a petri dish filled with water, and examined using transmitted light under a dissecting microscope at 10 – 15X magnification.

Each otolith was examined on two occasions, with at least a two-week interval between readings, and without prior knowledge of the length of the fish from which it originated. Each pair [one opaque (dark) and one hyaline (light)] of bands in sectioned otoliths was assumed to represent one growth season i.e. one year or annulus. Two methods were employed in order to test this. Firstly, the periodicity of band deposition was examined by means of tetracycline marking. In May 1994, individuals of *E. andersoni* (n = 8), *E. rivulatus* (n = 2), *E. marginatus* (n = 10) and *E. albomarginatus* (n = 1) were tagged with PIT (passive integrated transponder) tags, measured (TL mm), injected with 0.5 ml/kg body weight (as recommended by Lang and Buxton, 1993) of Terramycin®100 (oxytetracycline hydrochloride 100mg/ml) and kept captive in a variety of holding tanks at the Sea World aquarium facility in Durban. Body weights used to calculate dosages were estimated using length-weight relationships for each species (Chapter 2) and the length of the fish at time of injection. Some individuals were injected again after a period of 11-14 months to provide an additional reference mark in the otolith, and kept captive for a further period, before the fish were sacrificed and the otoliths collected. Additionally, individuals of *E. andersoni* (n = 21) and *E. marginatus* (n = 11) were measured, dosed with tetracycline, tagged with dart tags and released on a shallow reef off Durban in June 1994. Otoliths from injected fish were examined and photographed using an Olympus BH60 microscope with an epifluorescence HBO-100 watt WU filter block, producing final images of 40X magnification.

Validation of the periodicity of band deposition was also undertaken by means of marginal zone analysis (Hecht and Smale, 1986), whereby the margin of each otolith is examined and the frequency of occurrence of the opaque and hyaline bands on the otolith margin is plotted on a monthly basis.

Age estimates which coincided, or which did not differ by more than one year, were utilised to produce growth curves: if the estimates differed by one year, the average age was used for that fish. However, in the case of *E. rivulatus*, age estimates which differed by up to two years were used, as a large number of estimates would otherwise have been discarded (see Results). The average age was also used in this species. Reproducibility of the age estimates was assessed using an index of average percentage error (APE) (Beamish and Fournier, 1981):

$$100\left[\frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|Xij - Xj|}{Xj}\right]\right]$$

where:

N	=	no. of fish aged
R	=	no. of times each fish is aged
X_{ij}	=	ith age determination of the jth fish
X_j	=	the average age of the jth fish

Measurements of annulus radii, for the purposes of back-calculation, were not attempted, owing to the difficulty of ensuring that the otoliths were all sectioned through the exact same plane. Slight variation in the position of the cut through the nucleus of the otolith, or variation in the sectioning plane, have little consequence for age estimation, but may result in substantial differences in the measurement of growth zone increments (Williams and Bedford, 1974), which would therefore compromise the back-calculation procedure.

Growth curves

Growth curves were obtained by first fitting the Schnute (1981) growth model to the observed data, using an iterative, non-linear, minimisation procedure (Punt, 1992). The Schnute model incorporates all potential underlying growth models (Butterworth *et al.*, 1989), and, by means of an iterative process which incorporates testing by means of log-likelihood ratios (Draper and Smith, 1966), the most appropriate growth curve was subsequently selected. Two alternative error models (absolute and relative error) associated with the age-length data were tested, and the residuals were tested to see if their distributions were random and heteroscedastic. Estimates of parameters and their standard errors were respectively obtained by minimisation of the residual sums of squares using the simplex method (Nelder and Mead, 1965), and by using a conditioned, parametric bootstrap procedure (Efron, 1981). The computer programme PC-Yield implemented the above (Punt and Hughes, 1989). Selection of the most appropriate model fit was undertaken by minimising the combined (coefficients of variation)^2 of the model parameters and minimising the residual sum of squares, as well as by selecting the models with the fewest parameters (Punt, 1992). The Kolmogorov-Smirnov test was used to compare size and age frequency distributions and the *t*-test was used to compare mean lengths for a given age.

Mortality estimation

Estimates of total mortality rates for each species were obtained by constructing age-length keys using the aged samples, and combining these with the total length frequency distributions to produce an age frequency distributions of the total catch. These were used to produce length-converted catch curves of the natural log of age frequency against age, from which total mortality (Z) rates were estimated from the slope of the descending limb of the catch curve using least-squares regression (Ricker, 1975). Only fully-selected age classes (i.e. to the right of the age class at the top of the curve, which represents the age at full recruitment) were utilised for this, and age classes with very low numbers of samples were excluded (Pauly, 1984; Sparre and Venema, 1998).

Cooke and Beddington (1981) suggested that the catch curve procedure produces substantially biased estimates of Z if catch numbers per age class included in the regression are low, and proposed a statistically superior method:

$Z = \ln[1 + 1/(\bar{a} - a_f)]$

where: a_f is the age at full recruitment, represented by the point immediately to the right of the highest point on the catch curve (Pauly, 1984)
$\bar{a}$ is the mean age of all fully-recruited fish (i.e. age $a \geq a_f$)

For *E. rivulatus*, inappropriate estimates of Z were obtained by these methods (see Results), and an estimate of this parameter was obtained by the Powell and Wetherall method (Powell, 1979; Wetherall *et al.*, 1987) (Appendix 3).

Total mortality (Z) is a combination of natural mortality (M) and fishing mortality (F) i.e. Z = M + F. M was estimated for each species by the following methods:

1 $\ln M = -0.0152 - (0.279)(\ln L\infty) + (0.6543)(\ln k) + (0.463)(\ln T)$ (Pauly, 1980)

where $L\infty$ (cm TL) and k (yr^{-1}) are parameters from the special von Bertalanffy growth model and
T (°C) is mean annual sea surface temperature (Natal Sharks Board, unpubl. data; P/Bag X2, Umhlanga Rocks 4320, South Africa)

2 $M = 1.521/(Tm^{0.720}) - 0.155$ (Rikhter and Efanov, 1977)

where: Tm is the age (yrs) at 50% maturity obtained by substitution in the relevant growth equation

3 $M = -0.0189 + 2.06k$ (Ralston, 1987).

where: k is a parameter from the special von Bertalanffy growth model.

An estimate of F was then obtained from the difference between M and Z.

Results

General

Total numbers of otoliths collected from the northern and southern sampling regions were similar, except in the case of *E. andersoni*, from which fewer otoliths were sampled in the southern region (Table 4.1). The attempt to obtain 20 fish in each length class was only partially successful, as very small and very large fishes were not often present in catches (Table 4.2).

Table 4.1: Numbers of fishes from which otoliths were collected from northern and southern sampling areas on the KwaZulu-Natal coast. Samples from the Durban area were collected by research fishing and spearing.

Sampling area	*E. andersoni*	*E. rivulatus*	*E. marginatus*	*E. albomarginatus*
Northern	139	117	103	111
Southern	63	93	101	106
Durban	15	12	11	-

Table 4.2: Numbers of fishes per length class (TL mm) from which otoliths were collected on the KwaZulu-Natal coast (May 1995 to September 1997, inclusive).

Length classes	*E. andersoni*	*E. marginatus*	*E. albomarginatus*	Length classes	*E. rivulatus*
0	-	-	-	0	-
50	-	-	-	25	-
100	-	2	-	50	-
150	3	1	-	75	-
200	1	1	-	100	-
250	6	4	2	125	1
300	5	3	5	150	2
350	7	4	8	175	4
400	12	11	20	200	1
450	28	15	30	225	4
500	23	23	22	250	9
550	29	30	36	275	16
600	29	32	31	300	31
650	29	26	23	325	52
700	21	16	16	350	37
750	17	13	4	375	41
800	4	10	2	400	17
850	3	8	1	425	6
900	-	3	1	450	1
1000	-	4	-		
1050	-	1	-		
1100	-	2	-		
Total	217	209	215		222

An alternating series of opaque and transluscent bands was observed in most of the sectioned otoliths. In the tests for periodicity of growth zone deposition using tetracycline, only some of the captive individuals of the four species survived for longer than one year (Table 4.3). For *E. andersoni* and *E. marginatus*, therefore, the position of the tetracycline check marks indicated that a single annulus was deposited each year (Figures 4.1a,b). For *E. rivulatus* and *E. albomarginatus*, the evidence is less convincing, as the time interval between the dosing with tetracycline and the death of the fish was too short (Figures 4.1c,d). None of the fish that were dosed with tetracycline and released into the wild were recaptured.

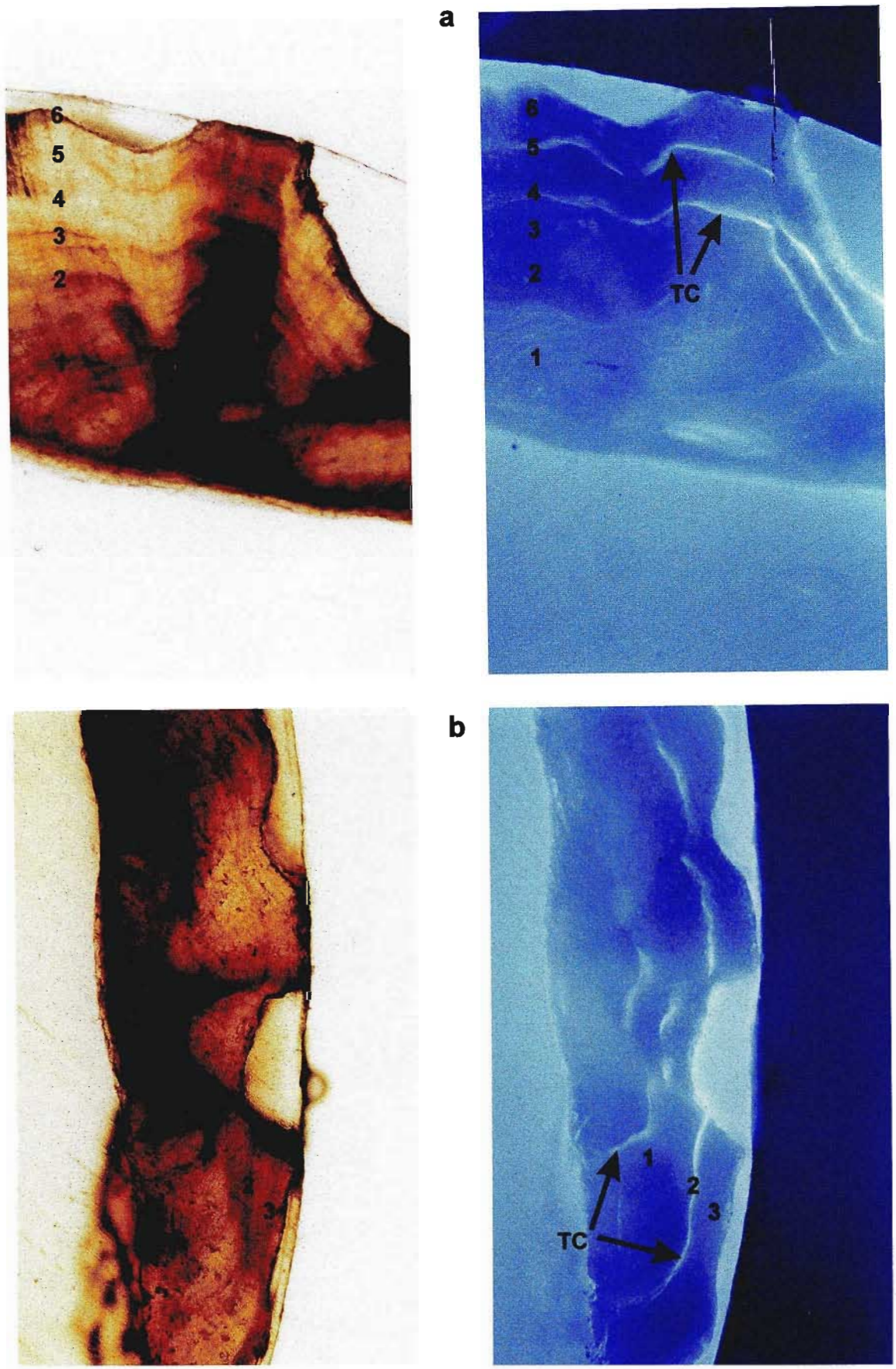


Figure 4.1: Photos of sectioned otoliths of fishes injected with tetracycline. Numerals indicate opaque bands, arrows indicate tetracycline (TC) check marks. Left image using transmitted light, right image using UV light.
(a) *E. andersoni*: Initial length and injection date: 445 mm, 11/05/94; second length and re-injection date: 622 mm, 05/06/95; final date and length: 25/12/97, 690 mm.
(b) *E. marginatus*: Initial length and injection date: 138 mm, 01/07/94; second length and re-injection date: 245 mm, 05/06/95; final date and length: 21/12/97,

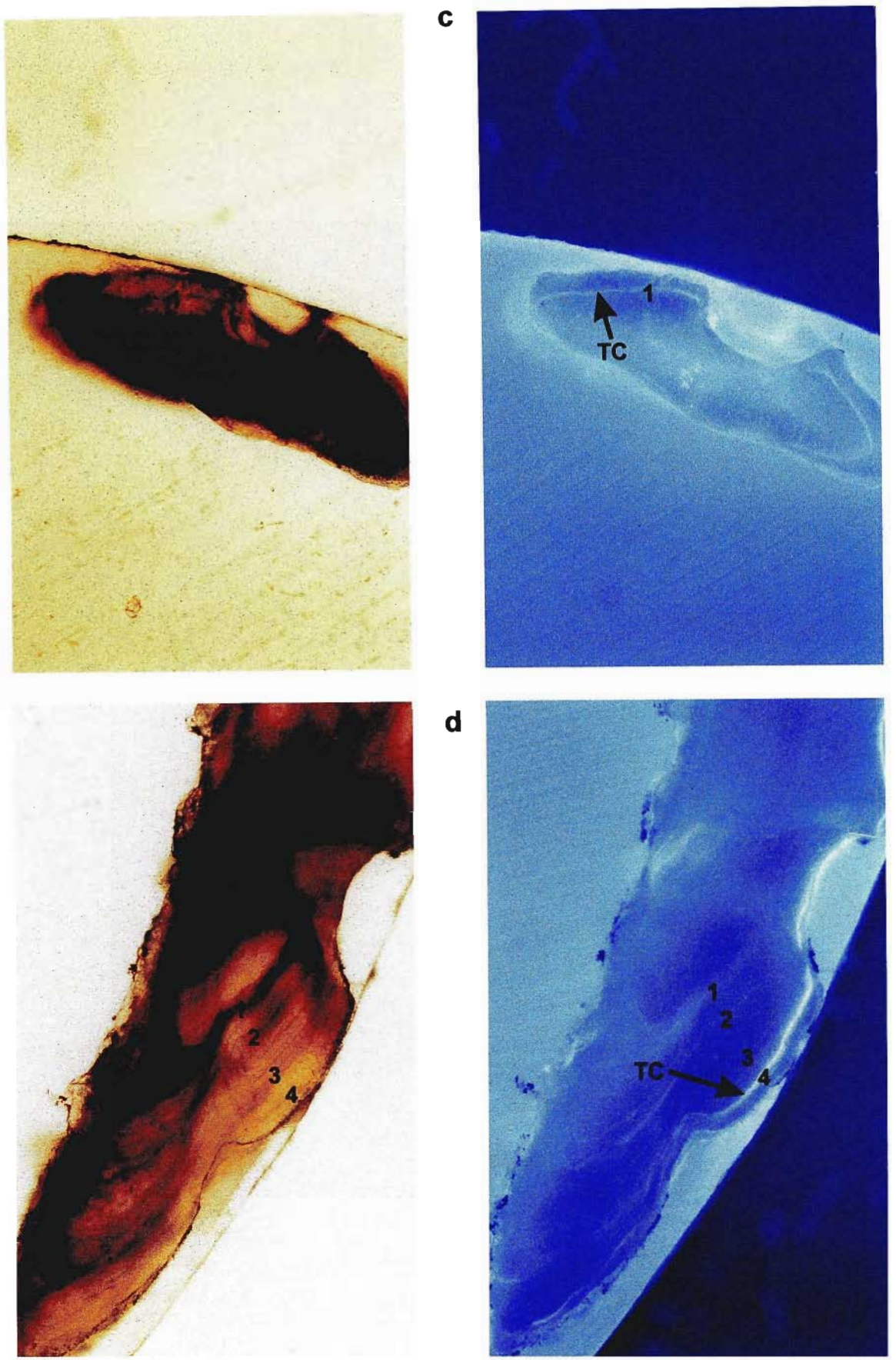


Figure 4.1 cont.: Photos of sectioned otoliths of fishes injected with tetracycline. Numerals indicate opaque bands, arrows indicate tetracycline (TC) check marks. Left image using transmitted light, right image using UV light.
(c) *E. rivulatus*: Initial length and injection date: 100 mm, 30/05/96; final date and length: 25/1/97, 130 mm.
(d) *E. albomarginatus*: Initial length and injection date: 235 mm, 18/06/96; final date and length: 06/12/96, 252 mm.

Table 4.3: Details of captive fishes that were injected with tetracycline. Months at "liberty" refers to the period post-injection that the fish were kept in captivity before they died or were sacrificed. In some fish there were two periods at liberty as they were injected twice. Growth (1) and (2) refer to the increase in length during each period of captivity. An asterisk * refers to otoliths of which photographs were taken (Figures 4.1a-d).

Species	Otolith code	Initial length (TL mm)	Months at "liberty" (1)	Growth (1) (mm)	Months at "liberty" (2)	Growth (2) (mm)
E. andersoni	A	123	3.3	30	-	-
E. andersoni	B*	445	14	177	18.7	68
E. andersoni	C	390	13	132	-	-
E. andersoni	D	360	6.5	25	-	-
E. andersoni	E	320	13	202	-	-
E. andersoni	F	315	13	190	-	-
E. andersoni	G	255	6.1	53	-	-
E. andersoni	H	270	6.9	94	-	-
E. rivulatus	I	235	9	10	-	-
E. rivulatus	J*	100	8	30	-	-
E. marginatus	K	314	17.5	49	-	-
E. marginatus	L	320	13	41	-	-
E. marginatus	M	335	13	52	-	-
E. marginatus	N	335	13	57	-	-
E. marginatus	O	257	13	61	9.5	10
E. marginatus	P	295	13	80	-	-
E. marginatus	Q	260	13	101	-	-
E. marginatus	R	113	11	162	14.5	56
E. marginatus	S	356	8	40	-	-
E. marginatus	T*	138	11	107	18	110
E. albomarginatus	U*	235	6	17	-	-

The attempts to validate the periodicity of opaque band deposition by marginal zone analysis were partly successful, in that an increased occurrence of opaque zonation on the otolith margin occurred at a reasonably well-defined time of the year (Figure 4.2). Thus, in *E. andersoni*, increased numbers of otoliths with opaque margins were noted in October; for *E. rivulatus*, opaque banding peaked in August; for *E. marginatus* in February and, for *E. albomarginatus*, from September to December. In these last two species, the incidence of opaque zone deposition on the otolith margins was never greater than hyaline deposition, hence the interpretation of annual periodicity is not as clear. This may be as a result of a paucity of numbers of younger age classes, in which analysis of the marginal zone is more precise (Manooch, 1987). Greater emphasis was placed on younger fish of these two species by excluding ages > 6 years, but this did not improve the validation of periodicity (Figure 4.2). In combination with the tetracycline marking experiment, however, it was concluded that an opaque zone is only deposited once a year in all four species, and hence the combination of an opaque and a hyaline zone was considered to represent one year's growth.

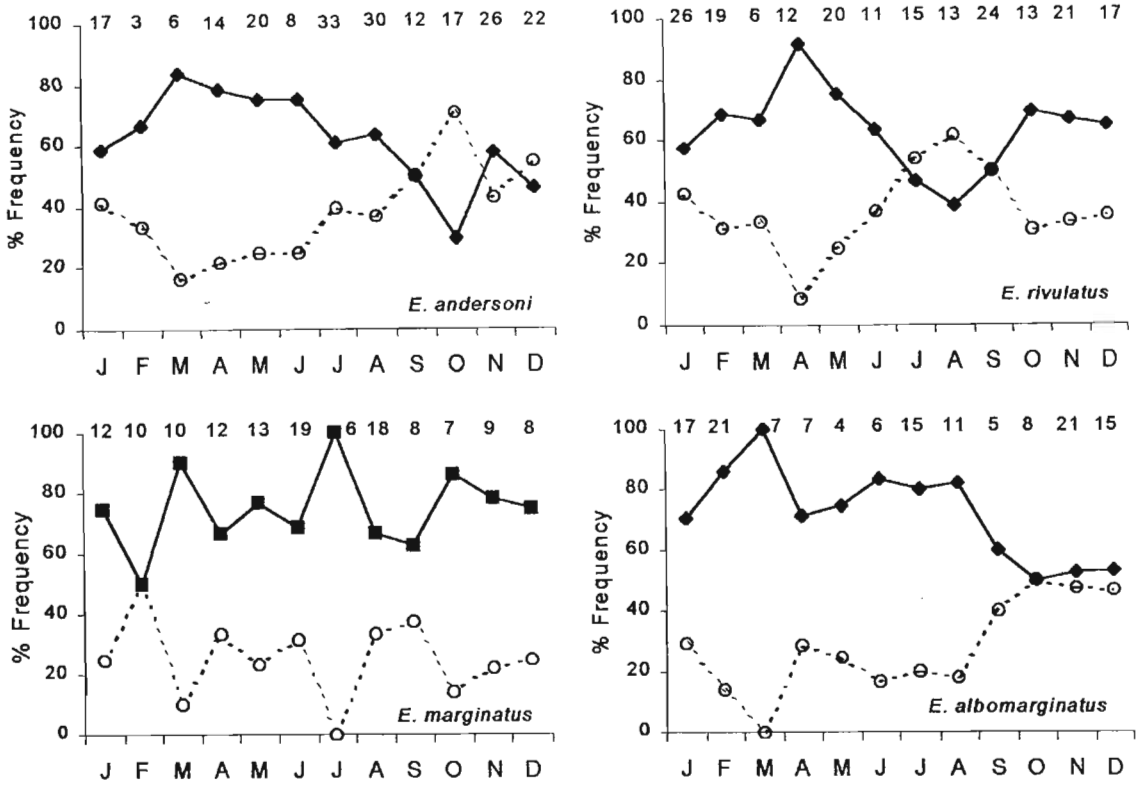


Figure 4.2: Frequency of occurrence of opaque (dotted lines) and hyaline zones (solid lines) on the margin of the otoliths of four species of serranids. Monthly sample numbers are indicated at the top of each graph. Monthly data were pooled for all years and sampling areas. For *E. marginatus* and *E. albomarginatus*, only otoliths with ages ≤ 6 years were used.

E. andersoni

Of the 217 otoliths collected, 6 were unreadable or had a discrepancy between the two age estimates of more than one year. The APE value was 6.3 %, indicating that there was a high level of precision in the two age estimates. There were no significant differences in mean length at age between females from the southern and northern sampling regions (Table 4.4). Mean lengths at age of immature bisexual fish from the southern region were also larger, and significantly so at ages 3 and 5 (Table 4.4). No otoliths were collected from mature bisexual (i.e. transitional) fish. Differences in mean lengths of males from the two regions were not tested as very few males were encountered in the southern region (n = 7; Chapter 3) and otoliths were only collected from three of these. A significant difference in mean length at age for males and females from the northern sampling region was only recorded in one age class (Table 4.4). There was a significant difference between the mean lengths of bisexuals (488 mm; n = 22), females (494 mm; n = 58) and males (573 mm; n = 40) from the northern sampling area, over the age range in which all three sexes were recorded i.e. ages 2-6 years inclusive (ANOVA, $F = 8$, $p < 0.001$).

Table 4.4: Results of *t* tests of observed mean lengths (TL mm) of *E. andersoni* per age class (Fn vs Fs: northern females vs southern females; Mn vs Fn: northern males vs northern females; Bn vs Bs: northern bisexuals vs southern bisexuals; Bn vs Fn: northern bisexuals vs northern females; Bs vs Fs: southern bisexuals vs southern females; Bn vs Mn: northern bisexuals vs northern males; all bisexuals were immature). Means and standard deviations (SD) have been rounded off for convenience. S* denotes significance at the 0.05 level; NS = not significant.

	Females – northern			Females – southern			Fn vs Fs		Males – northern			Mn vs Fn	
Ages	Mean	SD	n	Mean	SD	n	|t|		Mean	SD	n	|t|	
0	-	-	0	-	-	0	-	-	-	-	0	-	-
1	251	18	3	-	-	0	-	-	-	-	0	-	-
2	357	40	7	-	-	0	-	-	253	-	1	2.44	NS
3	414	56	16	420	79	8	0.2	NS	466	88	2	1.21	NS
4	500	62	14	503	76	12	0.13	NS	504	74	15	0.16	NS
5	573	61	12	600	51	9	1.1	NS	641	49	16	3.26	S*
6	631	65	9	677	58	4	1.27	NS	651	85	6	0.54	NS
7	656	85	5	-	-	0	-	-	694	82	4	0.67	NS
8	720	42	2	-	-	0	-	-	690	-	1	0.58	NS
9	-	-	0	-	-	0	-	-	-	-	0	-	-
10	-	-	0	-	-	0	-	-	760	-	1	-	-
11	750	-	1	-	-	0	-	-	-	-	0	-	-

	Bisexuals - northern			Bisexuals - southern			Bn vs Bs		Bn vs Fn		Bn vs Mn		Bs vs Fs	
Ages	Mean	SD	n	Mean	SD	n	|t|		|t|		|t|		|t|	
0	-	-	0	-	-	0	-	-	-	-	-	-	-	-
1	-	-	0	-	-	0	-	-	-	-	-	-	-	-
2	433	39	2	450	-	1	-	-	2.37	S*	3.77	NS	-	-
3	421	38	6	499	27	6	0.37	NS	0.29	NS	1.13	NS	2.35	S*
4	508	72	8	576	61	8	4.13	S*	0.29	NS	0.14	NS	2.26	S*
5	531	80	5	645	78	11	2.04	NS	1.2	NS	3.76	S*	1.48	NS
6	625	-	1	727	-	1	2.68	S*	0.1	NS	0.28	NS	0.69	NS
7	-	-	0	-	-	0	-	-	-	-	-	-	-	-
8	-	-	0	-	-	0	-	-	-	-	-	-	-	-
9	-	-	0	-	-	0	-	-	-	-	-	-	-	-
10	-	-	0	-	-	0	-	-	-	-	-	-	-	-
11	-	-	0	-	-	0	-	-	-	-	-	-	-	-

All sexes (including immature bisexuals) were subsequently combined, and age and length frequency distributions from the two areas were compared (Figure 4.3). These were not significantly different (Kolmogorov-Smirnov, D = 0.15 and 0.14, respectively; p = 0.05), indicating that the size and age structures of fish from the two areas were the same, although older fish (> 6 years) were absent from the southern samples. However, when size and age frequencies from all sampling areas (i.e. northern, southern and Durban areas) were combined and tested for differences by sex, males and females were significantly different (D = 0.307 and 0.276, respectively). This results from the absence of males in the smaller, younger age classes (Figure 4.4). Bisexuals and males were first observed at age 2 years; bisexuals did not occur beyond age 6, and, although males were more common in the older age classes, the oldest recorded fish was female (Figure 4.4).

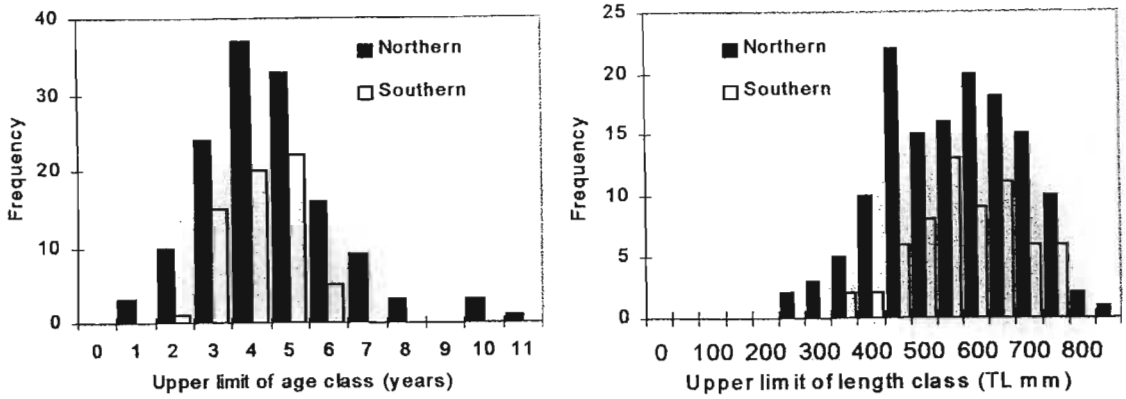


Figure 4.3: Age and length frequency distributions of *E. andersoni*, collected from northern (n = 139) and southern (n = 63) sampling areas. Females, males and immature bisexuals combined.

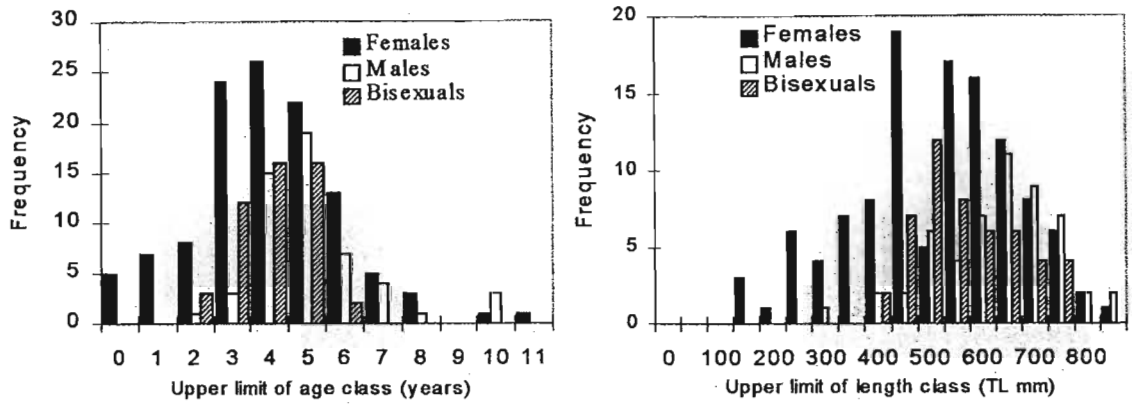


Figure 4.4: Age and length frequency distributions of female (n = 115), male (n = 53) and immature bisexual (n = 49) *E. andersoni*, based on all sampling areas (northern, southern and Durban areas).

Although there were differences in the age distributions of the sexes, the *t* tests suggested that age at length was the same for males and females, so they were combined with the bisexual fish in order to produce a growth curve. Having fitted several growth models to the observed age at length data using PC-Yield, three were selected for further testing (Table 4.5). These were chosen on the basis of their having residual differences between observed and predicted lengths that were both random and heteroscedastic. Growth models that failed to meet these criteria were excluded, as were those models that produced unrealistic estimates of $L\infty$.

Table 4.5: Models that initially provided an adequate description of the growth of *E. andersoni*, and estimates of their $L\infty$ and *k* parameters. Standard errors are in parentheses. An absolute error structure indicates that the variance of the ages is reasonably constant as age increases, whereas a relative error structure indicates that variance increases with age.

Model	No. of parameters	Error structure	$L\infty$ (TL mm)	*k* ($year^{-1}$)	Sum of squares	Combined CVs
General von Bertalanffy	4	Absolute	834 (4548)	0.315 (0.09)	945011	$\sim 7 \times 10^{10}$
Logistic	3	Relative	781 (31)	0.481 (0.03)	931527	78
Logistic	3	Absolute	765 (23)	0.52 (0.04)	923457	128

The von Bertalanffy model was subsequently excluded, as the L∞ value had a high standard error, indicating that this parameter was poorly estimated. Also, the number of model parameters, the sum of squared residual differences between observed and predicted lengths, and the combined coefficients of variation (CVs) were all higher for this model than for the other two models. The logistic growth model with a relative error structure was finally selected on the basis of its having a lower CV value (Figure 4.5):

$$L(t) = L\infty\left(1 - e^{-k(t-t^*)}\right)^{-1}$$

where: L(t) = length at time t
L∞ = 781 mm TL
k = 0.481 year^{-1}
t^* = 2.76 years (standard error = 0.20)

and where t^* is the age corresponding to the inflection point of the curve.

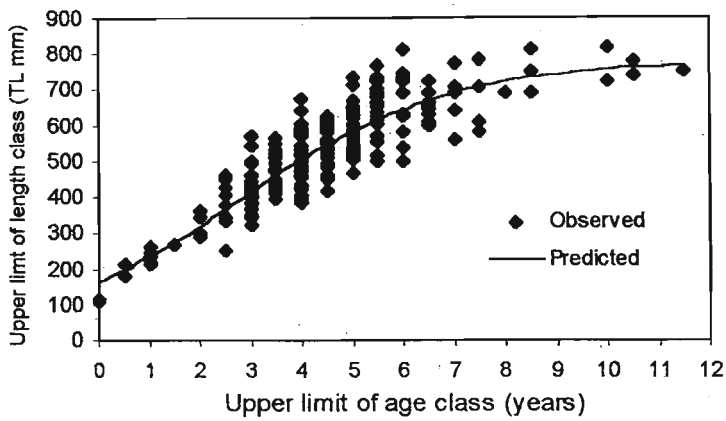


Figure 4.5: Logistic growth curve fitted to all age and length data (male, females and immature bisexuals) for *E. andersoni* (n = 217).

Mortality estimates are presented in Table 4.6. Estimates of M obtained by the Pauly (1980) and Ralston (1987) methods were high, and were excluded as the input parameters for these methods are derived from the von Bertalanffy growth model, which was found to be unsuitable to describe the growth of *E. andersoni*.

Table 4.6: Mortality estimates for *E. andersoni*. Values that were finally used are in bold. Values of parameters required for the estimations are provided, and are defined in the methods section.

Mortality type	Mortality estimate (yr^{-1})	Estimation method
Z^1	0.689	Catch curve (Figure 4.6)
Z^2	0.678	Cooke and Beddington (1981); a_f = 5 yrs, □ = 6.03 yrs
Z	**0.684**	**Average of Z^1 and Z^2**
M	0.647	Pauly (1980); L∞ = 78.1 cm, k = 0.481 yr^{-1}; T = 21.1°C
M	1.01	Ralston (1987); k = 0.481 yr^{-1}
M	**0.416**	**Rikhter and Efanov (1977); Tm = 3.9 yrs**
F	**0.268**	**Z – M**

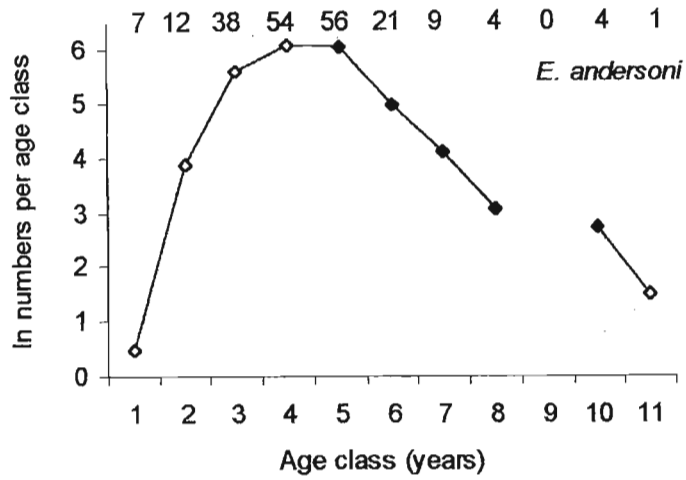


Figure 4.6: Catch curve for *E. andersoni*. Solid diamonds indicate points used to determine Z from the slope of the descending arm of the curve. Numbers of aged fish per age class are indicated on top of the graph.

E. rivulatus

Of the 222 otoliths collected, 33 were unreadable or had an age discrepancy of more than two years between the two readings. Of the remaining 189 otoliths, 48 (25 %) had a reading discrepancy of two years, but it was considered that if the discrepancy limit was set at one year, too many otoliths would be excluded. Of these 48 otoliths, 28 were from males and 20 were from females, while 35 were from the northern sampling region and 13 from the southern. Because of the potential bias created by the inclusion of disproportionately high numbers of these northern age estimates, the mean estimated ages of these otoliths (with a discrepancy of 2 years) from the two regions was tested. The estimates from both regions ranged from 4-17 years, and both had a mean age of 8 years (standard deviations: 3.5 and 3.6 for northern and southern regions, respectively). It was therefore considered that the inclusion of these otoliths would not bias comparisons of age estimates from northern and southern regions. The increased number and degree of discrepancy between the age estimates occurred because the otoliths of *E. rivulatus* were small and thick relative to the other three species, and were the most difficult to read. This is reflected in the higher APE value (10 %), indicating that the level of precision of the two age estimates was not as high as that of the other species.

Comparisons of mean length at age for subsets of the age-length data revealed that there appeared to be differences in growth between females and males, and between northern and southern sampling areas (Table 4.7). For each age class, and almost without exception, both females and males from the southern area were larger at a given age than their northern counterparts, and males were larger than females in both northern and southern areas. It was also apparent that mean length did not consistently increase with increasing age (Table 4.7), indicating that similar-sized fish could have quite different ages. No otoliths were collected from bisexual fish, which were very few in number (n = 6; Chapter 3). Age distributions were not significantly different between the two sampling regions (Kolmogorov-Smirnov, D = 0.15, p = 0.05; all sexes combined), but there was a significant difference between

length distributions of the aged samples from these areas (D = 0.41, p = 0.05; Figure 4.7). Similar comparisons revealed that both age (D = 0.41, p = 0.05) and length frequencies (D = 0.41, p = 0.05) differed significantly between males and females, with females dominating in the younger age classes, and age classes greater than 11 years being restricted to males only (all sampling regions combined; Figure 4.8). The youngest male was four years old.

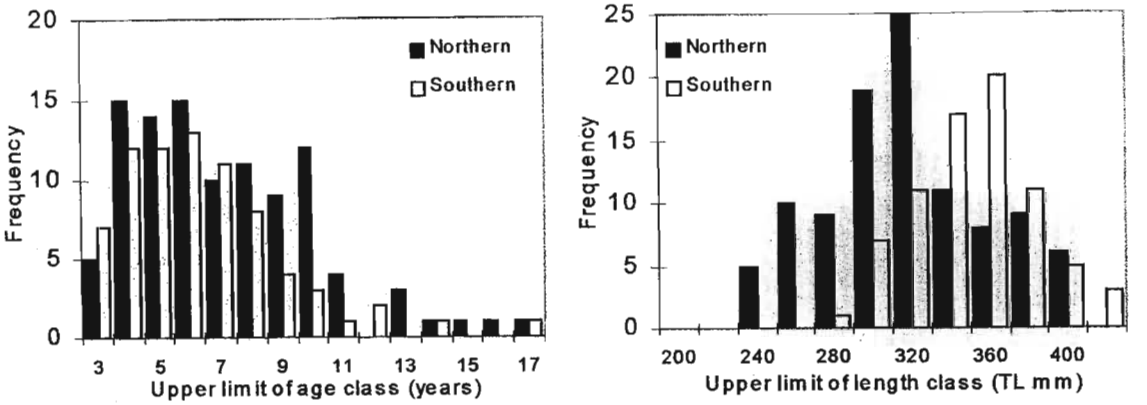


Figure 4.7: Age and length frequency distributions of *E. rivulatus*, based on subsamples used for age determination, collected from northern (n = 102) and southern (n = 75) sampling areas.

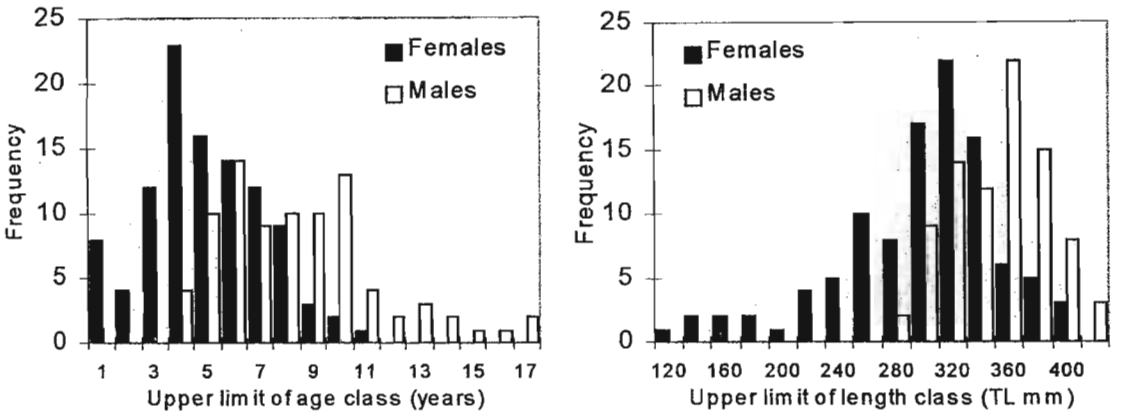


Figure 4.8: Age and length frequency distributions of female (n = 104) and male (n = 85) *E. rivulatus*, based on all sampling areas combined (northern, southern and Durban areas).

Attempts to fit growth models to subsets of the data (i.e. separate fits to males and females in each sampling region) were unsatisfactory, as the resultant growth curves were either linear or exponential. This is explained by the absence of smaller, younger fish, which were only sampled in the Durban region. Age estimates from these 12 "Durban" fish, all females, were therefore combined with the estimates from the northern and southern regions to produce a growth curve for each region based on combined sexes i.e. these 12 estimates were utilised for both regions.

Table 4.7: Results of *t* tests of observed mean lengths (TL mm) per age class of *E. rivulatus* (females and males: northern vs southern areas; northern and southern areas: females vs males). Means and standard deviations (SD) have been rounded off for convenience. S^{*} and S^{**} denote significance at the 0.05 and 0.001 level respectively. NS = not significant.

	Females								Males								Northern		Southern	
Ages	Northern			Southern					Northern			Southern					Male vs female		Male vs female	
	Mean	SD	n	Mean	SD	n	|t|		Mean	SD	n	Mean	SD	n	|t|		|t|		|t|	
3	277	29	5	312	24	7	2.29	S*	-	-	0	-	-	0	-	-	-	-	-	-
4	268	48	13	331	32	10	3.56	S**	333	53	2	367	13	2	0.87	NS	1.74	NS	1.46	NS
5	301	45	8	307	15	8	0.39	NS	304	29	6	363	7	4	3.96	S**	1.16	NS	7.02	S**
6	279	29	8	332	33	6	3.22	S**	326	38	7	344	14	7	1.17	NS	2.74	S*	0.88	NS
7	294	20	6	327	9	6	3.79	S**	353	26	4	359	11	5	0.49	NS	4.09	S**	5.1	S*
8	306	17	5	348	22	4	3.27	S*	312	23	6	362	21	4	3.47	S**	0.41	NS	0.89	NS
9	292	12	3	-	-	0	-	-	323	23	6	366	33	4	2.56	S*	2.12	NS	-	-
10	290	-	1	390	-	1	-	-	340	36	11	388	18	2	1.81	NS	1.31	NS	0.09	NS
11	323	-	1	-	-	0	-	-	331	24	3	342	-	1	0.39	NS	0.3	NS	-	-
12	-	-	0	-	-	0	-	-	-	-	0	369	27	2	-	-	-	-	-	-
13	-	-	0	-	-	0	-	-	357	45	3	-	-	-	-	-	-	-	-	-
14	-	-	0	-	-	0	-	-	385	-	1	360	-	1	-	-	-	-	-	-
15	-	-	0	-	-	0	-	-	364	-	1	-	-	-	-	-	-	-	-	-
16	-	-	0	-	-	0	-	-	309	-	1	-	-	-	-	-	-	-	-	-
17	-	-	0	-	-	0	-	-	379	-	1	406	-	1	-	-	-	-	-	-

Several models provided reasonable fits to the age-length data from the two sampling regions (Table 4.8), having residual differences between observed and predicted lengths that were random and heteroscedastic, as well as having realistic estimates of L∞. For the northern samples, the special von Bertalanffy model (Figure 4.9) was finally selected, as it had fewer parameters and a lower combined coefficient of variation (CV). For the southern samples, the general von Bertalanffy and Richards models were excluded as they had more parameters, high CV values, and, in the case of the latter model, the high standard error of the L∞ estimate indicated that this parameter was poorly estimated. Although the combined CVs for the logistic model were the lowest, and the sums of squares were slightly lower, the growth rate (*k*) was unrealistically high [serranids investigated to date have a *k* value between 0.1 and 0.6 year $^{-1}$ (Fishbase, 1998)], so this model was also excluded. Of the remaining two models, the special von Bertalanffy model with a relative error structure was ultimately selected (Figure 4.9), as it had a slightly lower CV.

Table 4.8: Models initially used to provide the growth of *E. rivulatus*, and their estimates of L∞ and *k*. Standard errors are in parentheses. An absolute error structure indicates that the variance of the ages is fairly constant as age increases, whereas a relative error structure indicates that variance increases with age.

Model	No. of parameters	Error structure	L∞ (TL mm)	*k* (year^{-1})	Sum of squares	Combined CVs
Northern						
General von Bertalanffy	4	Absolute	353 (18)	0.179 (0.109)	140230	4751
Special von Bertalanffy	3	Relative	332 (8)	0.394 (0.056)	142748	229
Southern						
General von Bertalanffy	4	Absolute	357 (6)	0.71 (0.13)	65308	~7 x 10^9
Richards	4	Absolute	355 (51657)	0.79 (0.19)	65274	49595
Logistic	3	Absolute	353 (5)	0.922 (0.095)	65339	177
Special von Bertalanffy	3	Absolute	362 (6)	0.53 (0.063)	65838	210
Special von Bertalanffy	3	Relative	366 (6)	0.477 (0.055)	66367	202

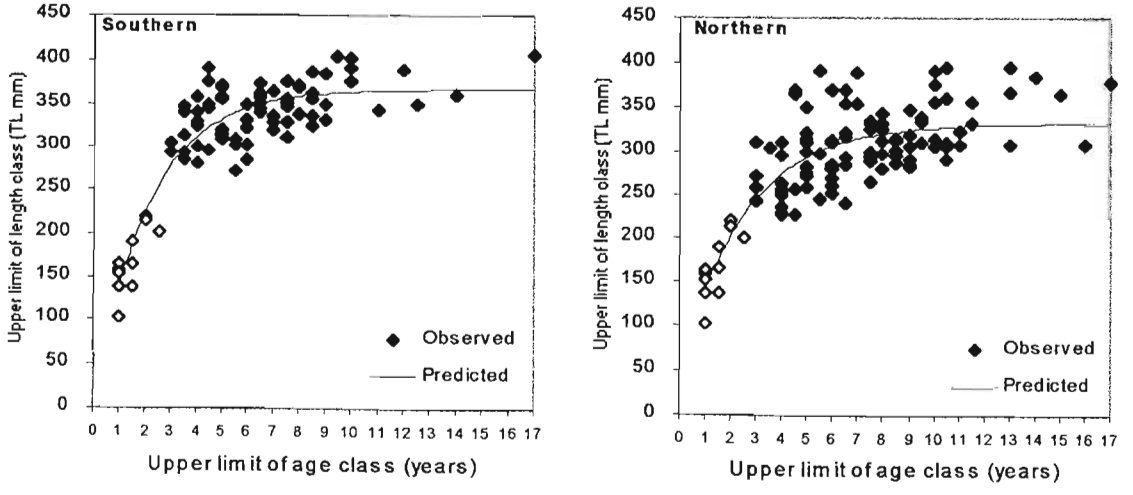


Figure 4.9: Special von Bertalanffy growth curves fitted to all age and length data (sexes combined) for *E. rivulatus* from the southern (n = 87) and northern (n = 114) sampling regions. The hollow diamonds represent 12 age estimates of fish from the Durban area which were combined with each region (see text).

The growth models are therefore represented by:

$$L(t) = L\infty\left(1 - e^{-k(t-t_0)}\right)$$

		Southern	Northern
where: $L\infty$	=	366 mm TL	332 mm TL
k	=	0.477 year^{-1}	0.394 year^{-1}
t_0	=	0.02 years (S.E. = 0.18)	-0.41 years (S.E. = 0.22)

and t_0 is the theoretical age at zero length.

Mortality estimates are presented in Table 4.9. Estimates of Z produced by the catch curve (Figure 4.10) and by the Cooke and Beddington (1981) method were far lower than all estimates of M in both sampling areas. Although high, the estimates of M are considered reasonable, since all three methods produced similar estimates. Furthermore, Mackie (1998) obtained an estimate of M of 0.994 yr^{-1} for this species from a relatively unfished area in Western Australia, and high M values are associated with low $L\infty$ values (Ralston, 1987). Despite varying the age at full recruitment, low Z values were still obtained, and estimates obtained using the catch curve and the Cooke and Beddington method were therefore considered unrealistic. This parameter was therefore estimated using the Powell-Wetherall method (Appendix 3).

Table 4.9: Mortality estimates for *E. rivulatus* from northern and southern sampling areas. Values that were finally used are in bold. Values of parameters required for the estimations are provided, and are defined in the methods.

Mortality type	Mortality estimate (yr^{-1})	Estimation method
Northern		
Z	0.286	Catch curve (Figure 4.10)
Z	0.311	Cooke and Beddington (1981); a_f = 7 yrs, □ = 9.74 yrs
Z	**1.121**	**Powell-Wetherall; Appendix 3**
M	0.726	Pauly (1980); $L\infty$ = 33.2 cm, k = 0.394 yr^{-1}; T = 21.4°C
M	0.831	Ralston (1987); k = 0.394 yr^{-1}
M	**0.68**	**Rikhter and Efanov (1977); Tm = 2.3 yrs**
F	**0.375**	**Z – M**
Southern		
Z	0.232	Catch curve (Figure 4.10)
Z	0.353	Cooke and Beddington (1981); a_f = 5 yrs, □ = 7.36 yrs
Z	**1.14**	**Powell-Wetherall; Appendix 3**
M	0.788	Pauly (1980); $L\infty$ = 36.6 cm, k = 0.477 yr^{-1}; T = 20.7°C
M	1.00	Ralston (1987); k = 0.477
M	**0.803**	**Rikhter and Efanov (1977); Tm = 1.9 yrs**
F	**0.276**	**Z – M**

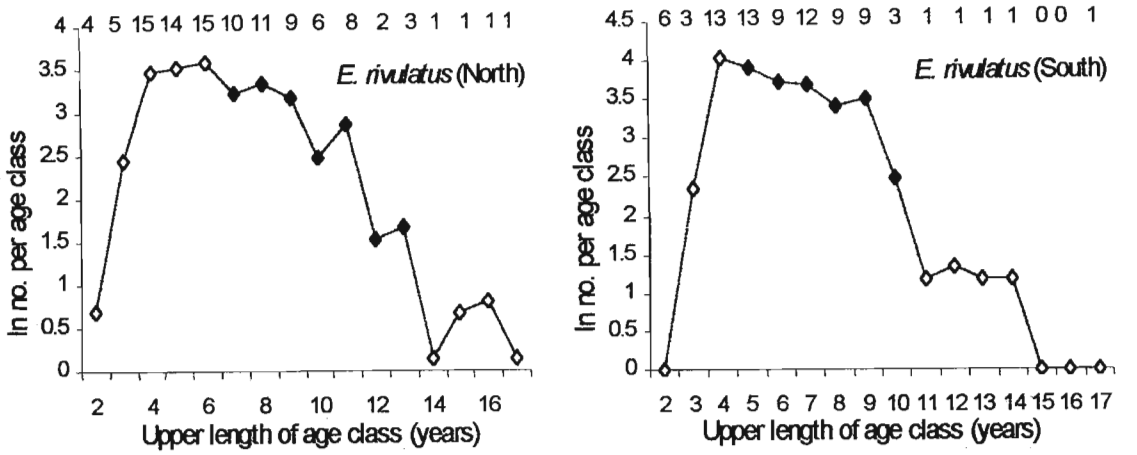


Figure 4.10: Catch curves for *E. rivulatus* from the northern and southern sampling regions. Solid diamonds indicate points used to determine Z from the slope of the descending arm of the curve. Numbers of aged fish per age class are indicated on top of the graphs.

E. marginatus

Of the 215 otoliths collected, 26 were unreadable or had a discrepancy between the two age estimates of more than one year. The APE value was 6.5 %, indicating that there was a high level of precision between the estimates. There were no significant differences in mean length at age between females from the northern and southern sampling regions (Table 4.10); differences in mean lengths of males from the two regions were not tested as very few males were sampled, particularly in the southern region (n = 2; Chapter 3). Only one immature bisexual fish was encountered (Chapter 3): this fish was 679 mm long and was aged at 7 years.

There were no significant differences in mean lengths at age between males and females in the northern sampling region, although very few males were obtained (Table 4.10). Age and length frequency distributions from the two areas were found to be not significantly different (Figure 4.11; Kolmogorov-Smirnov tests, D = 0.16 and 0.14 respectively; p = 0.05), indicating that the size and age structures of fish from the two areas were the same. However, age and length frequency distributions of males and females from all sampling areas combined (northern, southern and the Durban region) were significantly different (D = 0.95 and 0.93 respectively), because of the absence of males in the smaller/younger size classes (Figure 4.12). The youngest male was 9 years old, and although the oldest fish was a female of 16 years, males were more dominant in the older age classes (Figure 4.12).

Table 4.10: Results of *t* tests of observed mean lengths (TL mm) per age class of *E. marginatus* (females: northern vs southern areas; northern area: females vs males). Means and standard deviations (SD) have been rounded off.

	Females								Males						Northern	
Age	Northern			Southern					Northern			Southern			Male vs female	
	Mean	SD	n	Mean	SD	n	|t|		Mean	SD	n	Mean	SD	n	|t|	
1	245	1	2	-	-	0	-	-	-	-	0	-	-	0	-	-
2	352	20	3	-	-	0	-	-	-	-	0	-	-	0	-	-
3	421	71	4	429	39	10	0.28	NS	-	-	0	-	-	0	-	-
4	488	69	17	493	60	21	0.25	NS	-	-	0	-	-	0	-	-
5	540	72	24	570	49	20	1.58	NS	-	-	0	-	-	0	-	-
6	635	94	12	612	55	12	0.74	NS	-	-	0	-	-	0	-	-
7	623	73	6	658	104	10	0.71	NS	-	-	0	-	-	0	-	-
8	725	63	10	688	91	6	0.95	NS	-	-	0	-	-	0	-	-
9	709	55	6	733	-	1	0.4	-	810	-	1	890	-	1	1.69	NS
10	785	-	1	-	-	1	-	-	888	79	3	940	-	1	1.13	NS
11	-	-	0	-	-	0	-	-	1 020	-	1	-	-	0	-	-
12	-	-	0	-	-	0	-	-	895	-	1	-	-	0	-	-
13	-	-	0	-	-	0	-	-	853	-	2	-	-	0	-	-
14	-	-	0	-	-	0	-	-	940	-	1	-	-	0	-	-
15	-	-	0	-	-	0	-	-	-	-	0	-	-	0	-	-
16	-	-	0	910	-	1	-	-	-	-	0	-	-	0	-	-

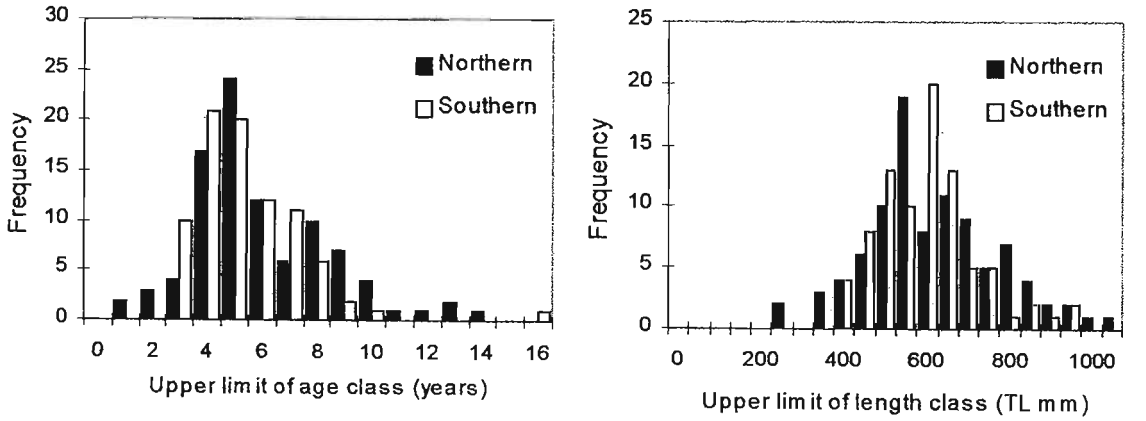


Figure 4.11: Age and length frequency distributions of *E. marginatus*, based on subsamples used for age determination, collected from northern (n = 94) and southern (n = 84) sampling areas.

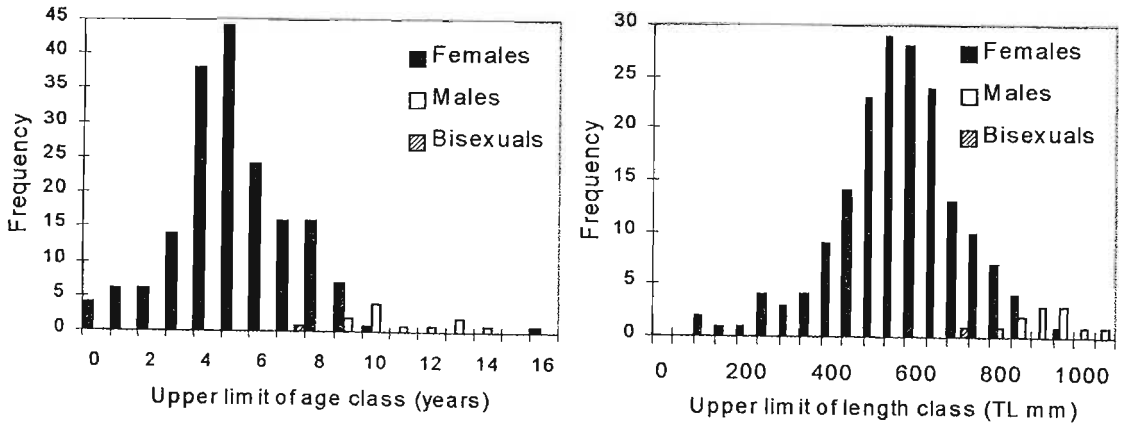


Figure 4.12: Age and length frequency distributions of female (n = 177), male (n = 11) and immature bisexual (n = 1) *E. marginatus*, based on all sampling areas.

When all the age and length data were combined, only one growth model, the general von Bertalanffy model, provided an adequate fit, with residual differences between observed and predicted lengths that were both random and heteroscedastic, and with a realistic estimate of L∞ (Table 4.11; Figure 4.13). The variance associated with the estimate of L∞ was high, however, indicating that this parameter is poorly estimated because of the paucity of fish in the larger size classes. Mortality estimates are presented in Table 4.12.

Table 4.11: Estimates of L∞ and *k* of the general von Bertalanffy growth model for *E. marginatus*. Standard errors are in parentheses.

No. of Parameters	Error Structure	L∞ (TL mm)	*k* ($year^{-1}$)	Sum of squares	Combined CVs
4	Relative	1070 (9630)	0.135 (0.067)	876075	10137

The growth equation is:

$$L(t) = L\infty\left(1 - e^{-k(t-t_0)}\right)^p$$

where: $L\infty$ = 1070 mm TL

k = 0.135 $year^{-1}$

t_0 = -2.66 years (SE = 12.1)

p = 1.57 (SE = 1807), where p is a constant (Schnute, 1981)

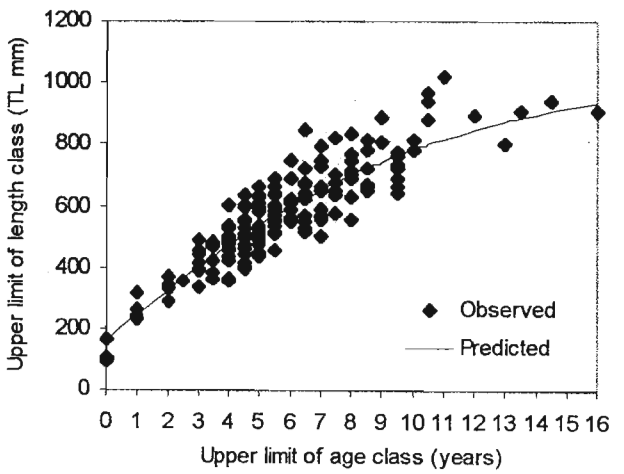


Figure 4.13: General von Bertalanffy growth curve fitted to all age and length data for *E. marginatus* (n = 189).

Table 4.12: Mortality estimates for *E. marginatus*. Values that were finally used are in bold. Values of parameters required for the estimation are provided, and are defined in the methods section.

Mortality type	Mortality estimate (yr^{-1})	Estimation method
Z^1	0.35	Catch curve (Figure 4.14)
Z^2	0.401	Cooke and Beddington (1981); a_f = 5 yrs, □ = 7.36 yrs
Z	0.375	Average of Z^1 and Z^2
M	0.258	Pauly (1980); L∞ = 107 cm, k = 0.135 yr^{-1}; T = 21.1°C
M	0.297	Ralston (1987); k = 0.135 yr^{-1}
M	0.24	Rikhter and Efanov (1977); Tm = 6.5 yrs
F	0.11	Z - M

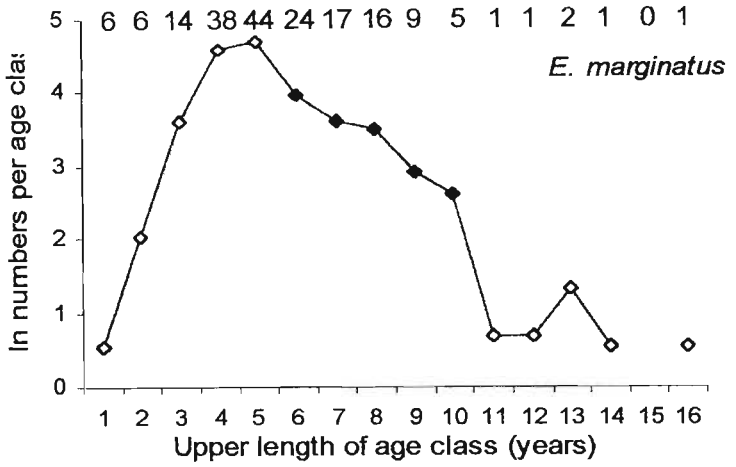


Figure 4.14: Catch curve for *E. marginatus*. Solid diamonds indicate points used to determine Z from the slope of the descending arm of the curve. Numbers of aged fish per age class are indicated on top of the graph.

E. albomarginatus

Of the 217 otoliths collected, 27 were unreadable or had a discrepancy of more than one year between the two age estimates. The APE value was 6.9 %, indicating that there was a high level of precision between the estimates. Apart from one age class, there were no significant differences in mean length at age between females from the northern and southern sampling regions, although fish from the southern region generally had a slightly larger mean size (Table 4.13). Differences in mean lengths of males from the two regions were not tested as no males were encountered in the southern region (Chapter 3).

There were no significant differences in mean lengths at age for males and females in the northern sampling region, although the sample size of males was very small, and males generally had a larger mean size (Table 4.13). Age and length frequency distributions from the two areas were compared, and were found to be significantly different (Kolmogorov-Smirnov tests, D = 0.41 and 0.25 respectively; p = 0.05), indicating that the size and age structures of females from the two areas were different (Figure 4.15). Age and length frequency distributions of males and females were also significantly different (D = 0.88 and 0.64, respectively), because of the absence of males in the smaller/younger size classes (Figure 4.16). The youngest male was 7 years old, and the oldest fish was a male of 16 years, although old females were also observed (Figure 4.16). Immature bisexual fish (n = 3) were observed at intermediate ages (4 to 8 years).

Table 4.13: Results of *t* tests of observed mean lengths (TL mm) per age class of *E. albomarginatus* (females: northern vs southern areas; northern area: females vs males). Ages were obtained for only three bisexual fish. Means and standard deviations (SD) have been rounded off for convenience. S* denotes significance at the 0.05 level. NS = not significant.

	Females								Males			Male vs female		Bisexual
Ages	Northern			Southern					Northern					
	Mean	SD	n	Mean	SD	n	|t|		Mean	SD	n	|t|		
2	300	26	4	281	79	4	0.45	NS	-	-	0	-	-	-
3	390	48	5	383	38	40	0.39	NS	-	-	0	-	-	-
4	459	63	18	483	44	21	1.37	NS	-	-	0	-	-	-
5	518	65	25	548	49	20	1.7	NS	-	-	0	-	-	448
6	570	61	15	626	41	6	2.08	NS	-	-	0	-	-	560
7	587	86	5	683	-	1	1.01	NS	525	21	2	0.94	NS	-
8	613	21	4	683	25	2	3.72	S*	-	-	0	-	-	735
9	606	73	4	-	-	0	-	-	694	45	2	1.51	NS	-
10	645	-	1	-	-	0	-	-	730	71	2	0.98	NS	-
11	730	-	1	-	-	0	-	-	-	-	0	-	-	-
12	767	66	2	-	-	0	-	-	-	-	0	-	-	-
13	800	-	1	-	-	0	-	-	-	-	0	-	-	-
14	810	-	1	-	-	0	-	-	-	-	0	-	-	-
15	-	-	0	-	-	0	-	-	860	-	1	-	-	-

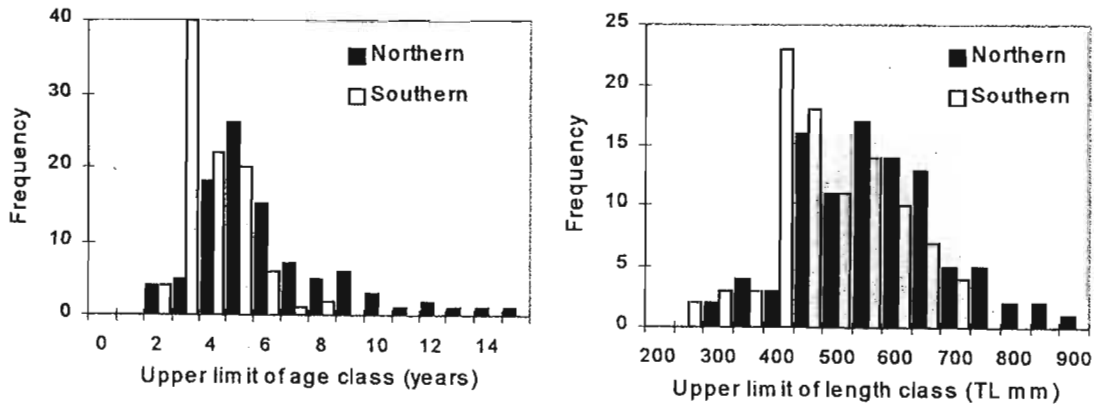


Figure 4.15: Age and length frequency distributions of *E. albomarginatus*, collected from northern (n = 95) and southern (n = 95) sampling areas.

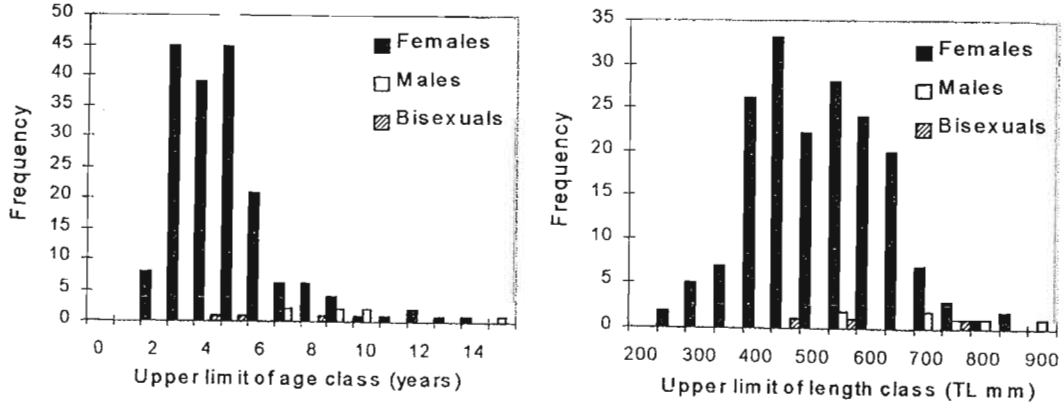


Figure 4.16: Age and length frequency distributions of female (n = 180), male (n = 7) and immature bisexual (n = 3) *E. albomarginatus* from all sampling areas.

When all the age and length data were combined, several growth models provided adequate fits, with residual differences between observed and predicted lengths that were both random and heteroscedastic, as well as producing realistic estimates of $L\infty$ (Table 4.14). The general von Bertalanffy and Richards models were excluded because they had more parameters, and the standard errors of the parameter estimates were high. The logistic model was excluded as both the sum of squared residuals and the combined CVs were higher than for the special von Bertalanffy model, which was ultimately selected (Figure 4.17). The mortality estimates are presented in Table 4.15.

Table 4.14: Models initially used to describe growth of *E. albomarginatus*, and estimates of their $L\infty$ and k parameters. Standard errors are in parentheses.

Model	No. of parameters	Error structure	$L\infty$ (TL mm)	k (year^{-1})	Sum of squares	Combined CVs
General von Bertalanffy	4	Relative	889 (1087)	0.115 (0.067)	535371	4291
Richards	4	Relative	736 (87273)	0.336 (0.091)	564180	~$5x10^{11}$
Logistic	3	Relative	713 (24)	0.454 (0.039)	581981	235
Special von Bertalanffy	3	Relative	789 (44)	0.214 (0.03)	545356	99

The growth equation is:

$$L(t) = L\infty\left(1 - e^{-k(t-t_0)}\right)$$

where: $L\infty$ = 789 TL mm
k = 0.214 year^{-1}
t_0 = 0.09 years (SE = 0.24)

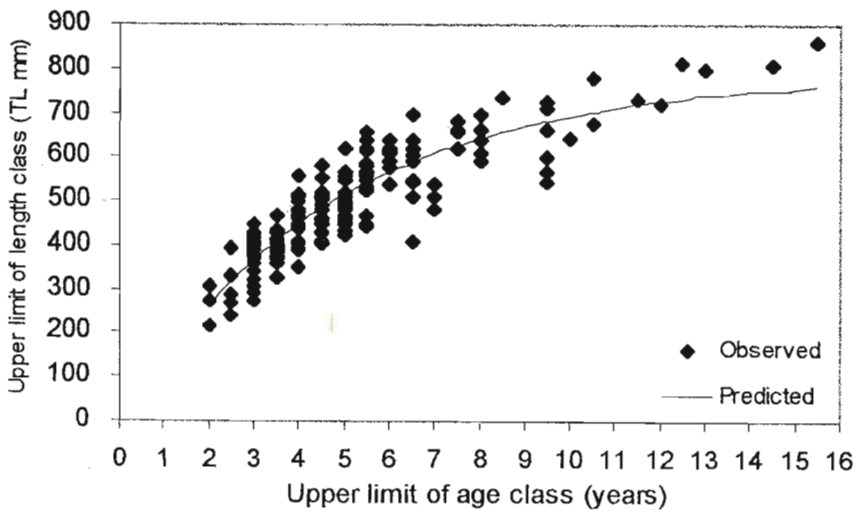


Figure 4.17: Special von Bertalanffy growth curve fitted to all age and length data for *E. albomarginatus* (n = 190).

In *E. rivulatus*, *E. marginatus* and *E. albomarginatus*, males were absent from the younger age classes, and became increasingly more abundant in the larger, older age classes, particularly for *E. rivulatus* and *E. marginatus*. For these two species, other studies have also shown higher mean male ages (Chauvét, 1988; Mackie, 2000). Significantly, no males of *E. rivulatus*, *E. marginatus* and *E. albomarginatus* were found below the minimum ages at maturity of the females for the respective species (Table 4.16), although in the case of *E. albomarginatus* from KwaZulu-Natal, the two ages were similar. For this species, however, female size and hence age at maturity estimates in KwaZulu-Natal waters may not be representative as a result of the low numbers of mature fish sampled, and because this area is at the edge of the distributional range of the species (Chapter 3). In this regard, the size at first maturity of females from Mozambique was much lower than for males (Table 4.16). Together with the histological evidence presented in Chapter 3, the lower female ages at maturity support the contention that all or most males are derived from mature females in these three species i.e. they are monandric protogynous hermaphrodites.

In *E. andersoni*, although the youngest age classes consisted of females, young males were also observed, and the male age at first maturity was lower than the female age at first maturity (Table 4.16), indicating that at least some males are not derived from mature females. Moreover, immature bisexuals were first recorded at the age of 2 years i.e. in an age class lower than the age at female maturity, indicating that some males were developing from the juvenile phase. Apart from the fish aged less than 3 years, there was complete overlap in age of females and males, and males were not more numerous in the older age classes than females. These observations provide good evidence for an alternative origin for some males, and, together with the observed fish in the process of changing sex from female to male, support the diagnosis of diandry in this species (Chapter 3).

Table 4.16: Estimates of minimum ages at maturity, derived by substituting the minimum lengths at maturity (Chapter 3) into the relevant growth model for each species.

Species	Minimum length at maturity (TL mm)		Minimum age at maturity (years)	
	Female	Male	Female	Male
E. andersoni	417	383	3	2.7
E. rivulatus	165	261	1.3	3.1
E. marginatus	545	800	5.1	10.5
E. albomarginatus	600	511	6.8	7
E. albomarginatus (Mozambique)	329	591	-	-

For all four species, males tended to be larger than females of the same age. Although these differences were seldom significant, perhaps because of the low numbers of males in some species and in some length classes, this suggests that some factor(s) may increase male growth relative to females. For example, behavioural differences that enhance male access to food could account for growth disparities. These may prove difficult to establish in the wild, owing to difficult diving conditions off the KwaZulu-Natal coast. Also, there is a potentially circular argument

here i.e. do males grow faster because they can access more resources, or can they access more resources because they grow faster (larger)?

An alternative explanation for growth disparity between sexes was proposed by Garratt *et al.* (1993), based on investigation of a protogynous sparid, who suggested that there is growth acceleration in males following sex change. Alternatively, the larger females in a particular age class may be changing sex, which would reduce mean female size in that age class. Evidence for the latter could include a larger mean size of transitional fish than females at the same age, although transitional fish were rare in this study. More intensive sampling of older age classes and transitional fish could help to clarify (1) whether size disparity between the sexes at a given age is a real phenomenon and (2) whether growth acceleration does in fact occur.

Notwithstanding Ricker's (1979) comments that none of the potential growth curves for describing growth have a biological basis, and that the only criteria for selecting a particular model are goodness of fit and convenience, the special von Bertalanffy growth model is typically used to describe growth in fishes. This trend has been perpetuated since Beverton and Holt (1957) incorporated the parameters into their yield per recruit model (Dr Daniel Pauly, University of British Columbia, 2204 Main Mall, Vancouver, Canada, pers. comm.). The frequent use of the special von Bertalanffy model does, however, allow for interspecific comparisons of growth estimates from different studies (Ricker, 1975). Justification for its choice as a growth model has been strengthened since Pauly (1981) demonstrated the biological basis for the parameterisation of the model, although this author noted that the four parameter general von Bertalanffy model is generally more appropriate for most fishes. Furthermore, Schnute (1981) and Moreau (1987) have demonstrated that there is a close relationship between all the various growth models, and that the von Bertalanffy and logistic models are, *inter alia*, different expressions of the same model. On this basis, the best-fitting growth curve was selected for each of the four species investigated here, rather than simply assuming that growth conformed to the special von Bertalanffy model. Ultimately, the general von Bertalanffy or the special von Bertalanffy model proved appropriate for three of the four species, with a logistic curve providing the best fit for *E. andersoni*. The use of a logistic model to describe growth in fishes is rare, and a survey of recent literature indicated that examples are restricted to species from southern Africa viz. a carangid *Lichia amia* (van der Elst *et al.*, 1993), a sciaenid *Argyrosomus inodorus* (Griffiths, 1996) and a sparid *Polysteganus undulosus* (Chale-Matsau *et al.*, 2000).

Estimates of total mortality (Z) obtained from catch curves are based on the assumptions that recruitment is constant, or at least that fluctuations are random and minor, and that total mortality is the same for all age groups used (partially overcome by only utilising the fully-recruited ages)(Ricker, 1975). The former assumption could not be verified in this study, although the observed slow growth rates and high longevities may dampen the effects of recruitment variability (Buxton, 1987). Combining samples from several years also averages out recruitment effects (Appeldoorn, 1996). For all four species examined here, the Z estimates obtained by the catch curve method and the method of Cooke and Beddington (1981) were similar to each other, so the use of an average of the two values is justified.

Estimation of natural mortality (M) is notoriously difficult (Gulland, 1988), and few other estimates are available for the species investigated here. Using the method of Pauly (1980), Mackie (2000) obtained an estimate of 0.99 $year^{-1}$ for *E. rivulatus* from Australia, and Bouain (1985) estimated M to be 0.1 $year^{-1}$ for *E. marginatus* in the Mediterranean. The M values for most serranids fall within the range of 0.09 $year^{-1}$ to 0.35 $year^{-1}$ (Fishbase, 1998). The Pauly method, which is based on species in temperate waters, has been questioned for its applicability to long-lived, tropical species (Mathews and Samuel, 1987). This method also tends to overestimate M for slow growing species and underestimate M for faster growing ones (Ralston, 1987). Approximate confidence intervals for Pauly's equations are large (0.61 to 1.63 times the estimate of M)(Gulland, 1984), indicating the uncertainty attached to the estimates. The confidence intervals for the method of Ralston (1987), are considerably lower (0.24 yr^{-1}), and this method may be a better estimator for serranids (Appeldoorn, 1996). However, both the Pauly method and particularly the Ralston method, consistently produced higher estimates of M than the Rikhter and Efanov method. More recent versions of the Pauly (1980) and Ralston (1987) methods (Pauly and Binohlan, 1996) did not produce substantially different values from the original versions. As will be discussed in the following chapter, lower estimates of M produce more conservative assessments of stock status, hence the Rikhter and Efanov estimates were preferred in this study.

The high M values obtained for *E. rivulatus* prevented the use of Z values estimated by means of a catch curve, which requires discussion. It is possible that the small size of this species has resulted in incomplete selection by the fishery, which tends to selectively target larger fishes. This is reflected in the shape of the catch curves for *E. rivulatus*, which are relatively "flat-topped" relative to those of the other three species i.e. the descending portions of the curve initially decline only gradually. Similar flat-topped catch curves were observed for groupers in the south-eastern United States, before the advent of commercial fishing (Huntsman *et al.*, 1999). In these cases, many of the age classes were well-represented, and numbers only declined at a late age, producing low Z estimates. The phenomenon is further complicated in *E. rivulatus* by the observed high variability in length at age, in turn exaggerated by the small size and high longevity of this species. The use of an age-length key to convert all lengths to ages may therefore not be appropriate, and the actual aged sample should be used to derive the catch curve. This was attempted, but results were not satisfactory, perhaps because the numbers of otoliths were low. The phenomenon of sex change may also confound the estimation of Z via a catch curve. Thus, the appearance of males, with observed increased growth rates, may alter the slope of the declining limb of the catch curve i.e. Z may change as a function of sex. A similar effect may have been obscured in the other two sex-changing species in this study, as numbers of males in these two were very low.

Maximum ages recorded in this study for *E. rivulatus* and *E. marginatus* (17 and 16 years, respectively) are substantially lower than those recorded elsewhere viz. 24 years for *E. rivulatus* from Australia (Mackie, 1998) and 36 years for *E. marginatus* from Tunisia (Chauvét, 1988). The absence of older ages in the South African fishes may be a consequence of fishing, which may selectively remove older, larger individuals from the population (Ricker, 1969; Miranda *et al.*, 1987; Russ, 1991; Coleman *et al.*, 2000). In support of this, an age of 24 years was obtained for a

specimen of *E. marginatus* from Mozambique (Fennessy, unpubl. data), where fishing effort was low when this fish was sampled (Chapter 3). Similarly, the maximum age for *E. rivulatus* in Australia was recorded in a specimen caught in a relatively unfished area (Mackie, 1998). It is possible that older fish may have been obtained in my study if sampling of local catches was more intensive. It is also noteworthy that, for reasons beyond my control, no otoliths were obtained from the two largest specimens of *E. marginatus* observed in this study (total lengths of 1125 mm and 1100 mm). Although speculative, estimates of ages from these otoliths may well have increased the maximum observed age for this species in KwaZulu-Natal.

There was a tendency for fish of all four species from the southern sampling region to be larger than their northern region counterparts at a given age, although the differences were only significant in the case of some of the age classes for *E. rivulatus*. A spatial disparity in growth rate may be anticipated in *E. andersoni* and *E. albomarginatus*, as almost no spawning of these species occurs in the southern region (Chapter 3), and hence more energy could theoretically be available for somatic growth (Stearns, 1992; Siems and Sikes, 1998). However, *E. rivulatus* and *E. marginatus* do spawn in the southern region and these fishes have larger mean sizes than their northern counterparts, which counters this argument. Mean sea surface temperatures from the two regions during the sampling period were very similar (T values, Table 4.9), and there was little seasonal disparity in temperatures (Figure 2.2, Chapter 2), which would appear to exclude temperature as grounds for growth differences between the regions. However, use of surface temperatures is misleading, since these fishes spend most of their time on the seabed, at depths mostly between 20 and 80 m (Chapter 2). Also, in the northern sampling region, occasional upwelling of cold water occurs, which results in the movement of cool (16°C) water onto the shelf (Lutjeharms *et al.*, 2000). This may affect growth of organisms in the region, but, as there have been no seasonal measurements of the upwelling process, temperature-related effects on growth are difficult to predict. Of potential relevance here is the work of Conover (1992) on *Menidia menidia* from the eastern United States, demonstrating faster growth for populations from high latitudes compared to those from lower latitudes. The disparity in growth rates was explained by the extremely short growing season experienced by high-latitude individuals that needed to grow rapidly if they were to survive the winter. This example may not be entirely appropriate, since *M. menidia* is a short-lived species, and the range in water temperatures experienced by this fish is extreme. It does, however, emphasise the influencing role of physical parameters on growth rates.

Alternatively, the greater length at age of the four serranids occurring in the southern region could have been accounted for by a greater availability of food resources there. This may have been a naturally greater abundance of prey, or a relatively greater availability as a result of density-dependent effects, i.e. greater fishing effort in the southern region has removed so many fish that there was more prey available for those that remained (Pitcher and Hart, 1982; Wyanski *et al.*, 2000). In support of this, there is an absence of older individuals of *E. andersoni* and *E. albomarginatus* in samples from the southern sampling region, which could indicate that fishing effort for these species is relatively higher there. An alternative explanation is that the older fish move away from this area (perhaps to join the northern populations where spawning occurs - Chapter 3). Conversely, sustained

high fishing effort in the northern region could have resulted in the observed spatial disparity in length at age in *E. rivulatus*, by the long-term selective removal of faster-growing individuals from several cohorts, thereby decreasing mean length (Wenner *et al.*, 1986; Bohnsack, 1990; Harris and McGovern, 1997). Thus, although the age structures of *E. rivulatus* in the northern and southern regions are the same, smaller size classes predominate in the former region, indicating that higher fishing effort for this species could have reduced the mean length for a given age. The F values obtained for the two regions suggest that fishing mortality is higher in the northern region. However, long-term length and age composition data from the two regions are required to resolve whether observed spatial differences in age structure are due to environmental or anthropogenic factors. Of relevance here is that genetically-mediated disparity in length at age as a result of fishing would require that the southern population is genetically isolated, which is unlikely given the predominant north-south current flow.

Growth parameters and observed ages obtained for the four species in this study indicate that these fish are relatively slow-growing and long-lived. Other ageing studies on epinepheline serranids show similar results, and are summarised in Table 4.17 for comparison. Note that the *k* (growth rate) parameter of the logistic growth model obtained for *E. andersoni* in this study is not directly comparable with that of the von Bertalanffy models, although estimates of $L\infty$ in the former model approximate those from the latter. The lowest recorded growth rate is that of *E. marginatus*, and the fastest that of *E. rivulatus*. The estimates of *k* obtained for *E. marginatus* and *E. rivulatus* in this study are similar to those obtained elsewhere (Table 4.17). Relative growth rates of the four species investigated in this study are graphically compared in Figure 4.19. Of the four species, the annual rate at which $L\infty$ is attained is slowest in *E. marginatus* and fastest in *E. rivulatus*. Thus, it takes *E. rivulatus* about three years to attain 80% of its $L\infty$, while for *E. andersoni*, *E. albomarginatus* and *E. marginatus*, the equivalent times are approximately 5, 8 and 12 years, respectively. The four species therefore represent a gradient in growth rate from slow to fast. As indicated in the introduction to this chapter, growth rate has implications for the rate at which fish can be harvested, and these will be discussed in the following chapter.

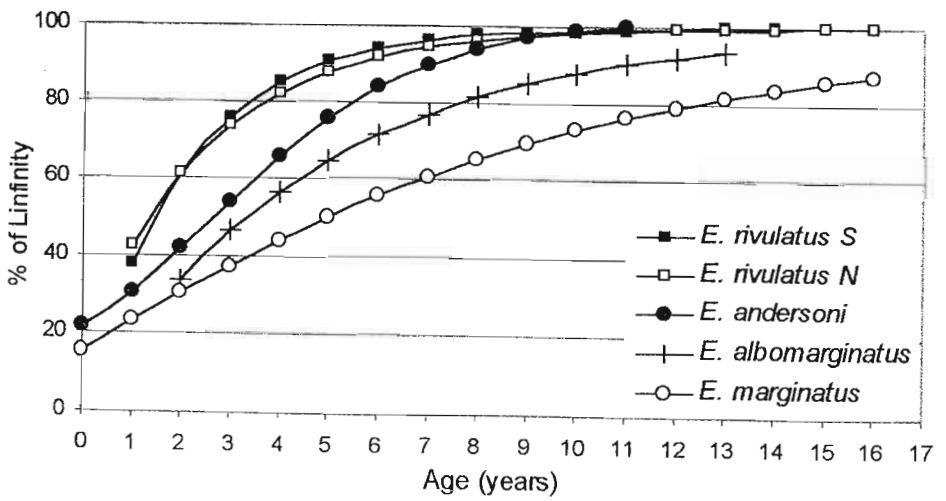


Figure 4.19: Plots of the percentage of $L\infty$ attained per year for four species of serranids, based on the most appropriate growth model for each species.

Table 4.17: Estimates of L∞ and *k* parameters for epinepheline serranids. Estimates are von Bertalanffy model parameters, except for those of *E. andersoni* that are from a logistic model. All sources are from Fishbase (1998), except [a]Rafail *et al.* (1969), [b] Bouain (1984), [c] Kara and Derbal (1995), [d] Bouchereau *et al.* (1999) and [e]Mackie (1998); bold estimates were obtained in this study. (S) and (N) for *E. rivulatus* refer to southern and northern sampling areas respectively.

Species	Area	L∞ (cm)	*k* (year^{-1})
Epinephelus adscensionis	Us Virgin Is	49.9 TL	0.11
Epinephelus aeneus	Morocco	85 TL	0.25
Epinephelus albomarginatus	**South Africa**	**78.9 TL**	**0.21**
Epinephelus andersoni	**South Africa**	**78.1 TL**	**0.48**
Epinephelus areolatus	Kuwait	39.1 TL	0.29
Epinephelus chlorostigma	Seychelles	66.9 TL	0.17
Epinephelus coioides	Kuwait	93 TL	0.17
Epinephelus diacanthus	Yemen	57 TL	0.21
Epinephelus drummondhayi	USA	97 TL	0.13
Epinephelus fasciatus	New Caledonia	23 SL	0.16
Epinephelus guttatus	Jamaica	52 TL	0.24
Epinephelus itajara	USA	201 TL	0.13
Epinephelus maculatus	New Caledonia	40 SL	0.28
Epinephelus marginatus	Tunisia	114.5 TL	0.09
Epinephelus marginatus[a]	Egypt	80 TL	0.11
Epinephelus marginatus[b]	Tunisia	197.8 TL	0.03
Epinephelus marginatus[c]	Algeria	78.5 TL	0.16
Epinephelus marginatus[d]	**France**	**135.9 TL**	**0.08**
Epinephelus marginatus	South Africa	107 TL	0.24
Epinephelus morio	USA	93.8 TL	0.15
Epinephelus nigritus	USA	239 TL	0.05
Epinephelus ongus	New Guinea	52.6 TL	0.33
Epinephelus rivulatus	**New Caledonia**	**27.9 SL**	**0.49**
Epinephelus rivulatus[e]	**Australia**	**30.7-33.8 TL**	**0.42-0.53**
Epinephelus rivulatus	South Africa (S)	36.6 TL	0.48
Epinephelus rivulatus	South Africa (N)	33.2 TL	0.39
Epinephelus striatus	Cuba	92.8 TL	0.10

CHAPTER 5: STOCK ASSESSMENT

Introduction

There are three categories of fishery assessment models: (1) surplus-production models, that require as input some measure of stock abundance (e.g. catch per unit effort); (2) age-structured models, that model the population dynamics of an age class of fish over time (e.g. yield per recruit models); and (3) dynamic biomass models that incorporate aspects of both of the former. Assessment of hook and line fisheries (also known as linefisheries) is generally undertaken using the second approach, because data requirements often render the other approaches unfeasible (Bannerot *et al.*, 1987; Punt, 1993; Appeldoorn, 1996). For example, few surplus production models have been undertaken for linefisheries, because accurate, long-term catch and effort data are rarely available, and the allocation of species-specific effort is difficult owing to the multispecies nature of these fisheries. Yield per recruit models, on the other hand, have frequently been used e.g. Huntsman *et al.* (1983), Matheson and Huntsman (1984), Sadovy (1989), Buxton (1992), Garratt *et al.* (1993), Huntsman *et al.* (1994), van der Walt and Govender (1996), Booth and Buxton (1997), Griffiths (1997a) and Chale-Matsau *et al.* (2000).

The yield per recruit (YPR) models are based on the assumption that the yield of the stock in one year is the same as the yield of a single age class (cohort) over its whole lifetime (Beverton and Holt, 1957). This, in turn, assumes that recruitment is constant from year to year; that selectivity of the fishery and maturity are "knife-edge" (i.e. all fish are recruited to the fishery at the same age, and all mature at the same age); that fishing mortality and natural mortality are constant; and that there is no emigration and immigration. The model further relies on the proviso that recruitment is independent of stock size. The model expresses the trade-off in yield between early harvesting, which implies loss of potential growth, and late harvesting, with potential loss of fish owing to natural mortality. Unlike the production models, the YPR model therefore implicitly incorporates two key processes (growth and natural mortality) which largely determine the biomass of the stock. The effects of fishing on reproductive output are incorporated in the derived spawning biomass per recruit (SBPR) model, which calculates the proportion of mature biomass remaining at various fishing mortalities and ages at capture. The equations for yield per recruit and spawning biomass per recruit are:

$$Y = \int_0^\infty FN(t).w(t).S(t)dt \qquad \text{and} \qquad SB = \int_0^\infty FN(t).w(t).Ma(t)dt$$

$S(t) = 0$ if $t < t_c$ $\qquad$ $Ma(t) = 0$ if $t < t_m$

$S(t) = 1$ if $t \geq t_c$ $\qquad$ $Ma(t) = 1$ if $t \geq t_m$

where:

Y	=	yield in mass
SB	=	spawning biomass
F	=	fishing mortality
N(t)	=	number of recruits R remaining after time t given by: $Re^{-M(t)}$ or $Re^{-(M+F.S(t))t}$ (where M is natural mortality)
w(t)	=	weight at time t given by: $a.[Lt = 1\text{-}e^{-k(t\text{-}t0)}]^b$ (where a and b are length-weight parameters, Lt is length at time t, *k* is growth rate, t_0 is age at zero length)

S(t) = knife-edged selectivity function (t_c = age at first capture)
Ma(t) = knife-edged maturity function (t_m = age at 50% maturity)

Although the actual number of recruits is unknown, by dividing both sides of each equation by R, the relative yield (Y÷R) and spawning biomass (SB÷R) per recruit will be obtained. The spawning biomass is simply the sum of the biomass at each age multiplied by the proportion mature at each age, and where the biomass is the product of the numbers and mean mass of individuals in the age class (Butterworth *et al.*, 1989).

Thus, although absolute yield and spawning biomass cannot be estimated, the effect on the stock of varying input parameters, such as fishing mortality and age at first capture, can be evaluated, which in turn can assist in the management of the fishery. For example, by plotting yield per recruit against fishing mortality (F), a maximum point on the curve can be obtained (maximum yield per recruit), attained at a fishing mortality level of F_{MAX}. If recruitment and mortality are assumed to be constant, this point is equivalent to the maximum sustainable yield (MSY) (Beverton and Holt, 1957) historically used as a reference point by fisheries managers, and F_{MSY} is the level of fishing mortality at which MSY is attained. The yield curves often attain an asymptote as F increases, suggesting (unrealistically) that infinite F can be applied to the stock. In this case the $F_{0.1}$ biological reference point is used, which implies that F is set at the level at which the slope of the yield per recruit curve is $1/10^{th}$ of the slope when F is zero (Gulland, 1968). This is a more conservative approach to setting levels of F for management purposes, and is thus warranted when a stock is particularly vulnerable to over-fishing (Punt, 1993).

The yield per recruit approach was designed to optimise the age at which fish are caught, so that growth over-fishing can be avoided i.e. to prevent poor yield as a result of fish being caught before they had sufficient time to grow. This approach does not account for the effects of fishing on reproductive potential, and these are evaluated by the spawning biomass per recruit (SBPR) model described above. This latter approach is designed to avoid recruitment over-fishing i.e. to ensure that the harvesting of fish does not severely compromise production of recruits for example by excessive harvesting of fish before they have had a chance to reproduce. Several biological reference points have been suggested as management measures when the SBPR approach is used. Butterworth *et al.* (1989) suggested that F should not increase beyond the level at which spawning biomass per recruit is reduced to 50% of the unfished level (F_{SBPR50}), although Clark (1993) recommended a level of F_{SBPR40}. Studies by Goodyear (1989), Clark (1991), Mace and Sissenwine (1993), Thompson (1993) and Mace (1994) have demonstrated that there is a strong likelihood of recruitment over-fishing and stock collapse when SBPR is reduced to 20-30% of the unfished level.

In this chapter, the results of the stock assessments for *E. andersoni*, *E. rivulatus*, *E. marginatus* and *E. albomarginatus*, undertaken by per recruit analyses, are presented and discussed in the light of the reference points referred to above.

Methods

Input parameters required for per recruit analyses for the four species were estimated in previous chapters and are summarised in Table 5.1. The age at first capture was set at the age (derived from the relevant growth equation) equivalent to the legal minimum size limit, i.e. 400 mm (TL) for *E. andersoni*, *E. marginatus* and *E. albomarginatus*. There is no minimum size limit for *E. rivulatus*, so the youngest, most well-represented age class was used instead. The sensitivity of the outputs to variability in natural mortality (M) was tested by including upper and lower M values represented by ± 50% of the likely M (derived in Chapter 4).

Table 5.1: Input parameters utilised in the per recruit models for four species of serranids from KwaZulu-Natal. Parameters are defined in the introduction. (N) and (S) denote northern and southern sampling areas respectively. $^{+}$ denotes the use of t^{*} from the logistic equation rather than t_0 from the von Bertalanffy equation.

Parameter	*E. andersoni*	*E. rivulatus* (N)	*E. rivulatus* (S)	*E. marginatus*	*E. albomarginatus*
F (yr^{-1})	0.268	0.375	0.276	0.135	0.24
M (yr^{-1})	0.416	0.746	0.803	0.24	0.228
$a \times 10^{-5}$	2.26	2.21	2.21	1.25	2.57
b	2.905	2.938	2.938	3.053	2.915
t_c (yrs)	3.1	4	4	3	3.4
t_m (yrs)	3.9	2.3	1.9	6.5	6.8
$L\infty$ (TL mm)	781	332	366	1 070	789
k (yr^{-1})	0.481	0.394	0.477	0.135	0.214
t_0 (yrs)	2.76^{+}	-0.41	0.02	-2.66	0.09

Outputs from the models were obtained using the computer programme PC-Yield (Punt and Hughes, 1989). Although per recruit calculations are generally based on the assumption that growth in weight is isometric, and that growth occurs according to the special von Bertalanffy model (Pauly, 1984), PC-Yield can also evaluate alternative growth models and mass-length relationships (Punt and Hughes, 1989).

Results

The outputs of the yield per recruit analyses are presented as plots of the percentage of maximum sustainable yield (MSY) obtained for a given fishing mortality (F) and at three levels of natural mortality (M). For *E. rivulatus*, the percentage of the yield at $F_{0.1}$ was used, as MSY is attained at high F values. Similarly, the spawning biomass per recruit outputs are presented as percentages of maximum spawning biomass i.e. as a proportion of that which occurs at the unfished level (F = 0).

E. andersoni

Over the range of potential M values tested, with estimated F and t_m values of 0.268 yr^{-1} and 3.9 years, respectively, current yields are 39-97% of MSY, with a likely level of 79%. To attain $F_{0.1}$ (0.374 yr^{-1}) at the likely level of M (0.416 yr^{-1}), current F can increase by 40%. SBPR levels are currently between 33-50% of the unfished level, and is likely to be at about 42% (Figure 5.1).

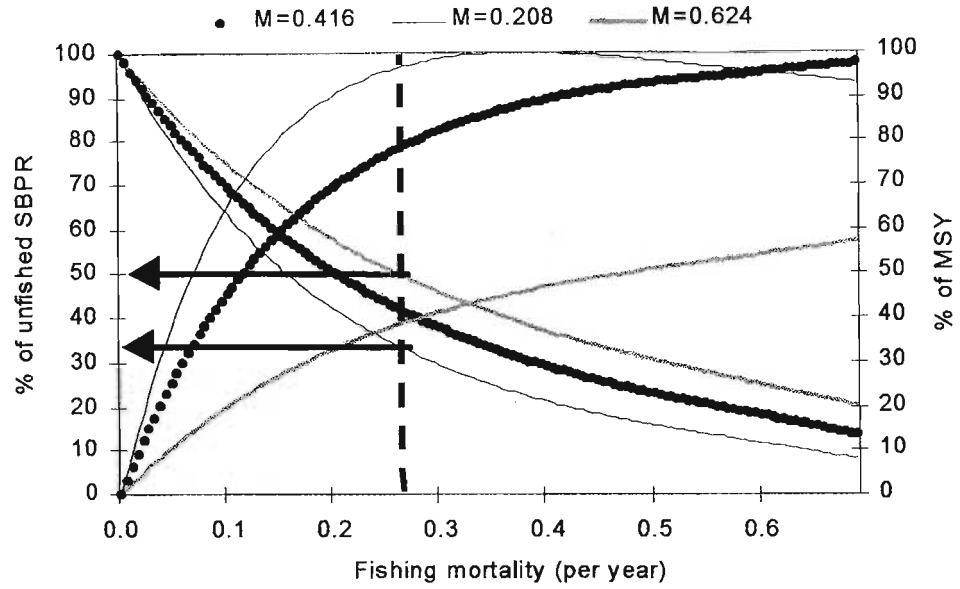


Figure 5.1: Per recruit outputs for *E. andersoni*. The dashed vertical line indicates current F (0.268 yr^{-1}). Arrows indicate potential SBPR levels at varying M levels (0.416 yr^{-1} ± 50%) and at current F.

E. rivulatus

In the northern sampling region, at an F level of 0.375 yr^{-1}, current yields are 12-82% of the yield at $F_{0.1}$, with a likely level of 38%. SBPR levels are 60-92% of the unfished level, and is likely to be at about 82% (Figure 5.2). In the southern sampling region, at an F level of 0.276 yr^{-1}, current yields are 7-66% of the yield at $F_{0.1}$, with a likely level of 23%. SBPR levels are 69-94% of the unfished level, and is likely to be at about 87% (Figure 5.3).

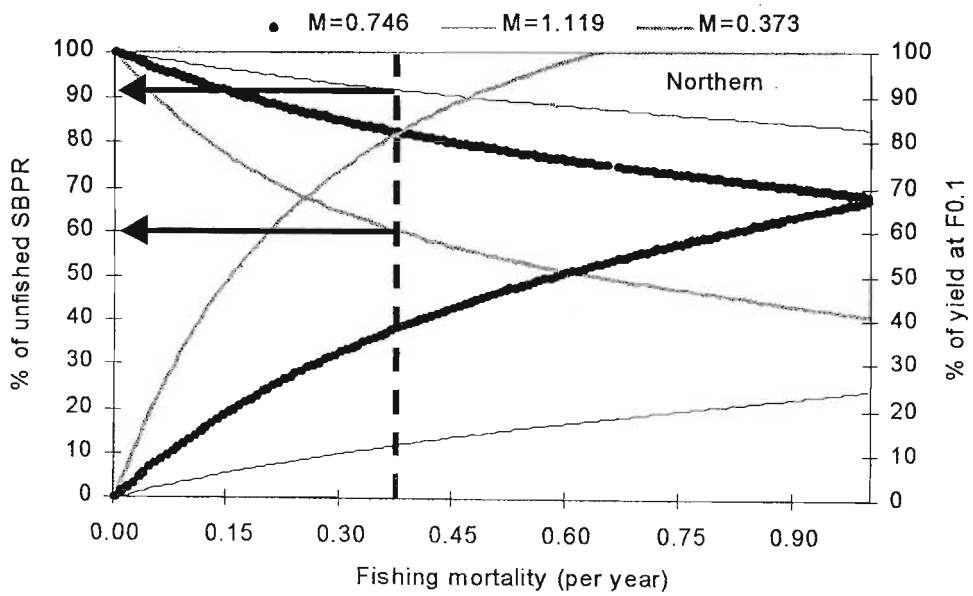


Figure 5.2: Per recruit outputs for *E. rivulatus* (northern sampling area). The dashed vertical line indicates current F (0.375 yr^{-1}). Arrows indicate potential SBPR levels at varying M levels (0.746 yr^{-1} ± 50%) and at current F.

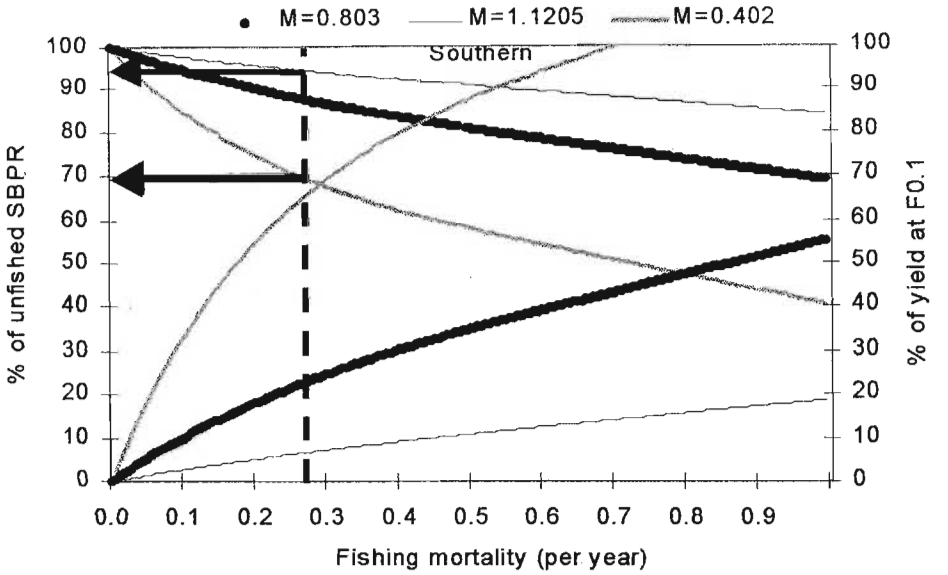


Figure 5.3: Per recruit outputs for *E. rivulatus* (southern sampling area). The dashed vertical line indicates current F (0.276 yr^{-1}). Arrows indicate potential SBPR levels at varying M levels (0.803 yr^{-1} ± 50%) and at current F.

E. marginatus

Over the range of potential M values used, and with an estimated F of 0.135 yr^{-1}, current yields are 54-100% of MSY, with a likely level of 86%. To attain $F_{0.1}$ (0.167 yr^{-1}) at the likely level of M (0.24 yr^{-1}), current F can increase by 24%. SBPR levels are 24-41% of the unfished level, and is likely to be at about 33% (Figure 5.4).

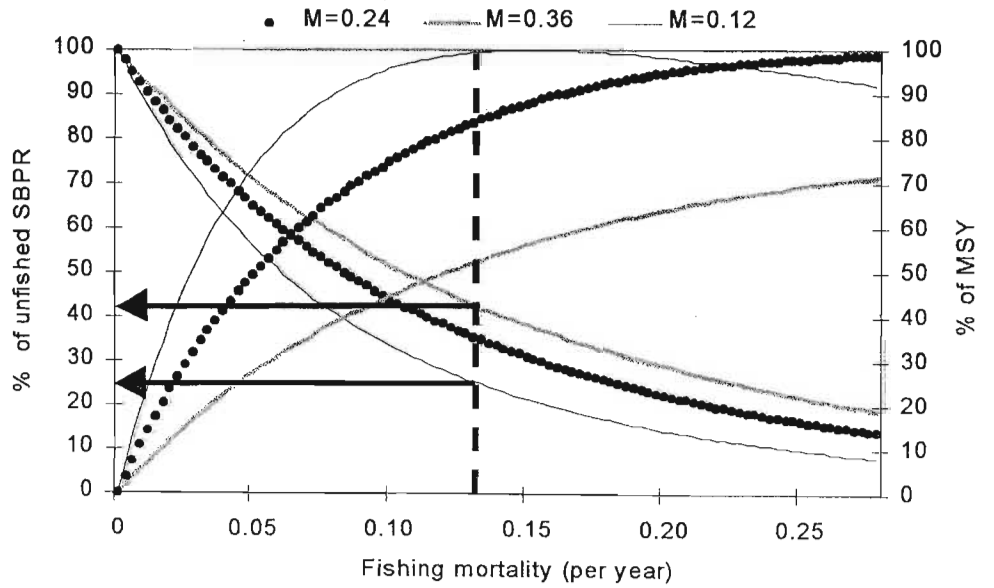


Figure 5.4: Per recruit outputs for *E. marginatus*. The dashed vertical line indicates current F (0.135 yr^{-1}). Arrows indicate potential SBPR levels at varying M levels (0.24 yr^{-1} ± 50%) and at current F.

E. albomarginatus

Over the range of potential M values tested, and at an estimated F of 0.24 yr^{-1}, current yields are 79-100% of MSY, with a likely level of 94%. To attain $F_{0.1}$ (0.224 yr^{-1}) at the likely level of M (0.342 yr^{-1}), current F must decline by 7%. SBPR levels are between 19-26% of the unfished level, and is likely to be at about 23% (Figure 5.5).

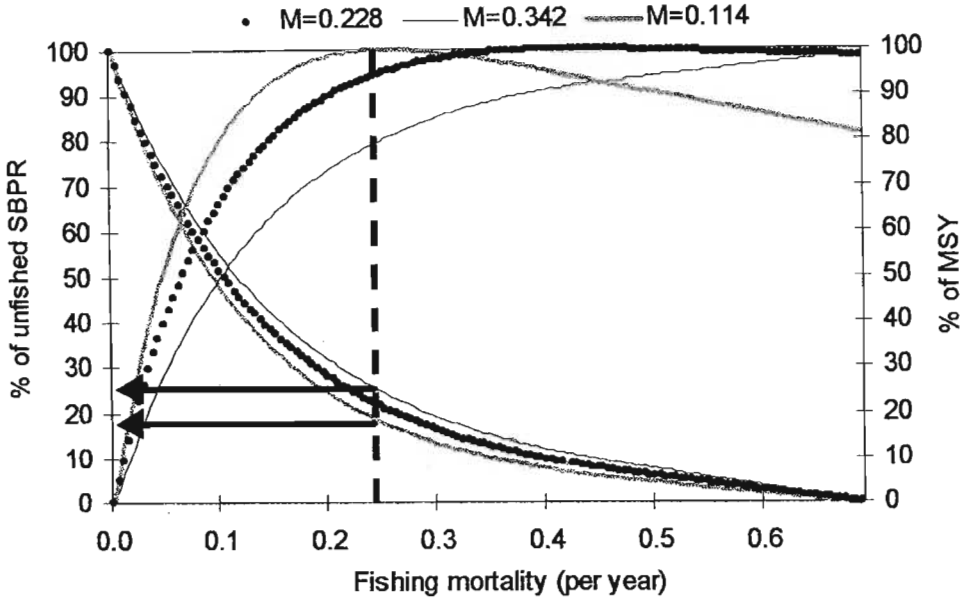


Figure 5.5: Per recruit outputs for *E. albomarginatus*. The dashed vertical line indicates current F (0.24 yr^{-1}). Arrows indicate potential SBPR levels at varying M levels (0.228 yr^{-1} ± 50%) and at current F.

Discussion

Based on the input parameters used, outputs of the per recruit models show that MSY is close to being attained for *E. andersoni*, *E. marginatus* and *E. albomarginatus*. To attain $F_{0.1}$, current F can increase substantially for *E. andersoni*, moderately for *E. marginatus*, but must decline for *E. albomarginatus*. Current SBPR levels for these species are all below 50% of the unfished levels, and are particularly low for *E. albomarginatus*. For *E. rivulatus*, however, F_{MSY} could not be estimated, and, according to the predictions of the model, current F can be greatly increased before $F_{0.1}$ is attained. SBPR levels for this species are also at high levels.

Although standard per recruit models incorporate two of the factors that strongly influence population biomass (i.e. growth and mortality), they do not address aspects such as inter- and intra-specific competition, or the fact that some fish may not spawn every year (Chapter 3). Per recruit analyses have also been criticised because the results only apply to equilibrium situations (listed in the introduction to this chapter), and particularly since they do not take account of variability in recruitment (Cushing, 1983). However, Huntsman *et al.* (1983) point out that, for long-lived reef fishes, carrying capacity and growth are likely to be more limiting than recruitment. Huntsman *et al.* (1994) further suggest that, provided there are no

trends in recruitment, the estimates of yield and spawning biomass should not be biased, but may have greater variance. However, other authors suggest that reef fish populations are recruitment driven (Plan Development Team, 1990; Doherty, 1991). No evaluation of recruitment trends was possible in this study, and the relationship between stock size and recruitment trends is unknown.

The assumption of knife-edged age at recruitment is probably violated for *E. andersoni*, *E. marginatus* and *E. albomarginatus*. Although the minimum size limit of 400 mm TL for these species is largely adhered to by fishers (pers. obs.), there is considerable variability in length at age. Discarding of sub-legal sized fishes also occurs, some of which do not survive, and these are not reflected in the catch curves. For *E. rivulatus*, too, this assumption is probably violated, as the flat-topped nature of the catch curve suggests that age at recruitment (t_c) varies from four to nine years (Chapter 4). This is probably because this species is not fully selected by the fishery owing to its small size. The outputs of the analyses showed varying sensitivity to the age at capture t_c. Using the likely level of M, when t_c was set at 5 years for *E. andersoni*, current F could be approximately doubled to attain $F_{0.1}$ or before SBPR was reduced to 40% of the unfished level. For *E. marginatus*, a t_c of 5 years meant that current F could increase by 70% to attain $F_{0.1}$, and needed to be reduced by 16% to attain F_{SBPR40}. For *E. albomarginatus*, a t_c of 5 years meant that current F could increase by 25% to attain $F_{0.1}$, but still needed to be reduced by 40% to attain F_{SBPR40}. The sensitivity of the *E. rivulatus* outputs to higher levels of t_c was not tested as it was apparent that inappropriate levels of potential F would result. The t_c values that were used in the final analyses for all four species were the most conservative from a stock assessment perspective, as they represented a "worst-case" scenario i.e. the species were assumed to be caught at a younger age than might possibly be the case.

The assumption of knife-edged age at maturity is violated, since individual fish of all four species matured over a range of lengths (i.e. ages). However, use of the age at 50% maturity averages this variability and is assumed to provide representative results. The assumptions of constant fishing mortality and natural mortality are difficult to evaluate, although the former is likely to have increased over the life span of the fishes that were sampled, as fishing effort increased over this period (Penney *et al.*, 1999). When the size at first capture is relatively large, constant natural mortality following recruitment to the fishery can reasonably be assumed (Appeldoorn, 1996). Finally, rates of immigration and emigration could not be evaluated, although limited tagging information for *E. andersoni* and *E. marginatus* suggests that these species are fairly resident (Appendix 2).

The outputs were fairly insensitive to the ages at 50% maturity (t_m) used. For *E. andersoni*, a conservative age of 3.9 years was used, although it could be as low as 3.2 years (equivalent to 430 mm TL). Use of the latter estimate would increase SBPR by about 15% at all three levels of M. Similarly, there is uncertainty regarding t_m for *E. rivulatus*. A likely lower value would also increase SBPR levels for this species, although this was not evaluated as SBPR levels were already high. The value of t_m used could also be over-estimated for *E. albomarginatus*, as few mature fish were sampled. The length at maturity for this species in South Africa was estimated at 600 mm TL (6.8 years), compared to a length of 341 mm TL obtained

for Mozambican samples. Assuming growth of these fish is similar to the South African fish i.e. the same growth model applies, t_m for the Mozambican fish is about three years. If this value is used in the SBPR model, the likely SBPR level is about 35% of the unfished level. This assumes that the South African fish mature at the same length/age as their Mozambican counterparts, but, as was discussed in Chapter 3, there is no evidence to support this.

Although the YPR outputs from the analyses were sensitive to the range of M values selected, the SBPR outputs were, with the exception of *E. rivulatus*, reasonably robust. The latter outputs were highly variable for this species because the initial selected values of M were high. Also with the exception of *E. rivulatus*, and particularly for *E. marginatus* and *E. albomarginatus*, attainment of MSY and rapid depletion of SBPR occurred at low levels of F. This was reflected in the relative slopes of the per recruit curves, the gradients of which were shallow for *E. rivulatus*, were increased in *E. andersoni* and again in *E. marginatus*, and attained their steepest slope in *E. albomarginatus*. The shallow slopes in *E. rivulatus* indicate that there is little variation in per recruit values over a wide range of fishing mortalities. It should be also noted that outputs of SBPR simply refer to levels of mature biomass per recruit, and hence do not incorporate a fecundity function i.e. the model takes no cognisance of the possibility that larger fish make a proportionally greater contribution to reproductive output by producing more eggs than smaller fish (Sadovy, 1996). If the four species investigated here have disproportionately high fecundities at older ages, this could mean that the current SBPR outputs are positively biased.

Serranid stocks characteristically produce most of their yield at low levels of F (Huntsman *et al.*, 1983; Goodyear, 1988; Ralston, 1987; Sadovy, 1994; Huntsman *et al.*, 1994). This trend is evident for two of the four epinepheline species investigated here. Thus, at the current low F levels for *E. marginatus* and *E. albomarginatus*, MSY has been attained, or is close to being so. For *E. andersoni*, if a conservative M level is assumed, MSY is also close to being attained. For *E. rivulatus*, a considerable increase in F is possible before MSY is reached. Of particular relevance to *E. rivulatus* are the cautionary comments by Pauly (1984) about applying management measures to small tropical species based on YPR alone, since high values of F are required to maximise YPR in these species. However, using F_{MSY} as a management target is of doubtful value, since, as has already been stated, this strategy takes no cognisance of the effects of fishing on the reproductive status of the stock. The MSY concept has been severely criticised (Larkin, 1977; Ludwig *et al.*, 1993; Mace, 1999), and rates of fishing mortality significantly below F_{MSY} have become the norm (Caddy and Mahon, 1995), following the adoption of the precautionary approach to fisheries management (Garcia, 1994; United Nations, 1995). Annex 2 of this last-cited report recommends that harvesting be constrained "... within safe biological limits within which the stock(s) can produce maximum sustainable yield (MSY)." F_{MSY} should therefore be seen as a barrier that must not be crossed. Conservative approaches, such as the $F_{0.1}$ strategy referred to in the introduction to this chapter, are therefore more appropriate. Mace and Sissenwine (1993), however, note that this strategy may not always be sufficient to prevent recruitment over-fishing. In *E. albomarginatus*, for example, current F is close to $F_{0.1}$ and yet the current SBPR level is low.

Serranids characteristically also experience a substantial reduction in reproductive capacity at low levels of F (Huntsman and Schaaf, 1994). This is particularly marked for *E. marginatus* and *E. albomarginatus* that have SBPR levels at about 30% and 20% of the unfished level, respectively. Huntsman *et al.* (1994) and Huntsman *et al.* (1999) consider that, for serranids, a reduction in SBPR to 30% of the unfished level constitutes over-exploitation. Together with the other biological reference points outlined in the introduction to this chapter, this suggests that *E. marginatus* and *E. albomarginatus* are over-fished in KwaZulu-Natal. For *E. andersoni*, the SBPR level of about 40% indicates that exploitation of this species is currently optimal. Based on the SBPR analyses presented here, *E. rivulatus* is only lightly exploited, probably because it is a small species that is not as desirable as the larger species, and hence is not fully selected by the fishery. From a SBPR perspective, it is problematic that *E. marginatus* and *E. albomarginatus* are harvested for several years before they attain maturity i.e. t_c is much lower than t_m. This has probably resulted in recruitment over-fishing for these species. For *E. andersoni*, t_c is not much smaller than t_m, while in *E. rivulatus*, t_c is much larger, so recruitment over-fishing is currently unlikely, particularly for the latter species.

The application of standard per recruit models to protogynous species may have biased results (Bannerot *et al.*, 1987; Huntsman and Schaaf, 1994; Sheperd and Idoine, 1993). Underlying this assertion is the premise that fishing selectively removes larger individuals i.e. males (Koenig *et al.*, 1996), which in turn can result in a "shortage" of this sex i.e. there is the potential for sperm limitation (Smith, 1972; Buxton, 1992; Sadovy, 1994). Briefly stated, simulation modeling has demonstrated that standard YPR models may overestimate F_{MSY} for those protogynous species that don't have a compensatory mechanism to minimise sperm limitation e.g. an increased rate of sex change if males are removed (Bannerot *et al.*, 1987). These authors also suggested that protogynous fish have greater reproductive output than gonochorist fish if sperm is not limiting.

Huntsman and Schaaf (1994) reinforced some of the findings of Bannerot *et al.* (1987), and also by means of simulations, demonstrated that, when fishing occurred, reproductive potential declined particularly rapidly in protogynous species, even at low values of F. If compensatory mechanisms to reduce sperm limitation existed, then reproductive potential declined identically in gonochorists and protogynous fish. The models of these latter authors also showed, however, that at high levels of M, there was little difference in the effects of fishing on reproductive potential between the two. The evidence presented in earlier chapters suggests that three of the species investigated here are monandric protogynous hermaphrodites (*E. rivulatus*, *E. marginatus* and *E. albomarginatus*). The fourth, *E. andersoni*, demonstrates some capacity for sex change, but most males appear to be arise from the immature female phase i.e. it is diandric. In monandric protogynous species, particularly those that have been exploited for some time, the sex ratio is often female-biased (Shapiro, 1987), as evidenced in *E. marginatus* and *E. albomarginatus*. One of the problems with standard SBPR analyses is that they rely on an equivalence of numbers of males and females, and the calculations are based on female biomass (i.e. potential egg production) alone. Hence the SBPR analyses currently do not account for declines in male biomass that may cause

severe reductions in spawning potential (Coleman *et al.*, 2000), and hence the analyses may overestimate actual spawning biomass per recruit (Sheperd and Idoine, 1993). This loss in reproductive potential due to differential loss of males has only been modeled, (Bannerot, 1984; Huntsman and Schaaf, 1994), as empirical demonstration has greater data requirements than currently exist (Huntsman *et al.*, 1999).

The extent to which monandric protogynous species can compensate for the removal of males, for example by increasing the rate of sex change or reducing the size at sex change, theoretically determines the extent to which the stock can be harvested (Bannerot *et al.*, 1987; Huntsman and Schaaf, 1994). It is unclear whether such compensatory mechanisms exist for the species investigated here. The size at sex change between populations of the four species is variable, suggesting that the process is socially-mediated (Shapiro, 1987), and hence the potential to reduce size at sex change at least exists. Insufficient numbers of male *E. marginatus* and *E. albomarginatus* from KwaZulu-Natal were obtained in order to draw meaningful comparisons between size at sex change in this area and in Mozambique, where only limited fishing had occurred at the time of sampling. No comparative data for *E. rivulatus* were available. However, the sex ratio for *E. marginatus* in the heavily exploited area was much more female-biased than in Mozambique, suggesting that the ability of this species to increase the rate of sex change is limited. Again, there are no comparative data available for the other species. It is of significance too, that if the rate of fishing is sufficiently high, then, even if the ability to compensate exists, the rapid removal of fish means that the compensatory process may be negated (Vincent and Sadovy, 1998). These authors quote an example of a protogynous sparid *Chrysoblephus puniceus* from KwaZulu-Natal (Garratt, 1993), and suggest that transition to males may not have kept pace with exploitation. Koenig *et al.* (1996) also mention the possibility that fish in the process of changing sex could be removed differentially, since they adopt male characteristics before the transition is completed (Shapiro, 1987). This, too, would mask compensatory efforts by the fish.

The absence, or inability, of compensatory mechanisms to maintain reproductive potential therefore would mean that, for the monandric protogynous species investigated here, standard per recruit analyses are likely to overestimate SBPR levels. Thus, the current stock status of *E. marginatus* and *E. albomarginatus* in KwaZulu-Natal is possibly lower than presented here (despite the use of conservative levels of natural mortality and age at first capture). *E. andersoni* is diandric, with possibly most males arising from the immature female phase, and therefore appears to have better withstood the effects of harvesting. The status of *E. rivulatus* is far more positive, since, although protogynous, this species grows fast and matures early, and is too small to be fully available to the fishery. This will be discussed in the following chapter, along with further considerations of the applicability of per recruit models to sex-changing species.

Notwithstanding the uncertainties associated with per recruit models described above, there is some independent evidence that the stock assessments undertaken in this chapter may be accepted with a degree of confidence. In Chapter 2, historical data were presented which showed significant reductions in mean lengths and/or

changes in length frequencies of catches of *E. marginatus* and *E. albomarginatus* over a 10 year period in KwaZulu-Natal. For *E. andersoni* and *E. rivulatus*, no such reductions were apparent. Additionally, there were significant and substantial differences in mean lengths and length frequencies between catches of *E. marginatus* and *E. albomarginatus* from KwaZulu-Natal and Mozambique. The latter area had been lightly fished at the time of sampling. The potential problems with comparisons of this nature are acknowledged in Chapter 2, but the comparisons indicate that fishing has apparently had a significant effect on the size structure of *E. marginatus* and *E. albomarginatus* in KwaZulu-Natal. This is supported by the opinions of some of the commercial fishers in this province, who have indicated that they have observed changes in catches and sizes of these two species over time (Appendix 1).

Many other fish species caught by the South African linefishery, particularly members of the Sparidae and Sciaenidae, have also been categorised as over-exploited i.e. their SBPR levels are at 30% or lower of the unfished level (Griffiths, 1997b; Mann, 2000). The four serranids caught by the linefishery in KwaZulu-Natal have been subjected to the same high fishing effort and, with the exception of *E. rivulatus* and, to a lesser extent, *E. andersoni*, their stocks have responded in a similar way.

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSIONS

In order to condense the information in this dissertation into a form that will facilitate a general discussion, résumés of the life histories of *E. andersoni*, *E. rivulatus*, *E. marginatus* and *E. albomarginatus* will be presented. This will be followed by a comparison of the key features of each species, and the implications of these for the resilience of the species to harvesting. Finally, some fisheries management issues will be discussed.

Epinephelus andersoni

A summary of the life history and other characteristics of this species is given in Table 6.1. *E. andersoni* is a subtropical species, endemic to the east coast of South Africa and southern Mozambique. It is the most common serranid recorded in catches in the province of KwaZulu-Natal, particularly in the northern region. It occurs at depths from the shore down to about 90 m, and is thus available to all sectors of the reef fishery, namely shore angling, spearfishing and recreational and commercial skiboat fishing. This species is particularly targeted by the skiboat sector because of its tasty, valuable flesh, and because it is readily caught. It is a medium-sized species, attaining a weight of about 8 kg.

E. andersoni demonstrates several features atypical of the protogynous hermaphroditic pattern reported for virtually all epinepheline serranids to date. It has no bimodal length or age frequencies for males and females; some males mature earlier and at a younger age than females; the mean lengths of males and females are not significantly different; and the sex ratio differs significantly from unity, but is dominated by males. However, very small, young males were not recorded, and numerous bisexual fish, including a few fish in the process of changing from female to male, were encountered. Several inactive bisexual fish were recorded at sizes and ages less than the length and age at first maturity of females. Thus, unlike the vast majority of epinepheline serranids investigated to date, in which males only originate from mature females, male *E. andersoni* can also originate from small, immature females. The features described here imply that *E. andersoni* does not have to undergo sex change to produce males.

However, the occurrence of some individuals with mature elements of both male and female tissue indicates that sex change can and does occur. Hence, there are two pathways by which males can originate, which constitutes diandric protogynous hermaphroditism. It was not possible to determine which pathway is followed more frequently, although the male-biased sex ratio and the large numbers of male and inactive bisexual fish at sizes smaller than the female size at maturity suggest that the immature female to male route is more common.

E. andersoni spawns over an extended period in the spring and summer. There is no unequivocal evidence to suggest that this species forms extensive spawning aggregations, although unusually large catches are occasionally made during and soon after the spawning season. Only one of these catches was sampled, and comprised mainly post-spawning fish. Almost no spawning was recorded in the southern sampling region, for reasons that are not entirely clear.

Table 6.1: Summary table of life history and other characteristics of *E. andersoni* established during this study. All lengths are TL. KZN = KwaZulu-Natal.

Distribution	Southeast African endemic
Biogeography	Subtropical
Residency	Potentially high
Catch methods	Skiboat fishing (mainly), spearfishing, shore angling
Local importance and value	Most commonly caught serranid in commercial and recreational skiboat catches; high value
Depth range	1 – 90 m
Maximum length and age in this study	816 mm; 11 yrs
Maximum weight in this study	6.8 kg
Bimodal length or age frequency for sexes	No
Length at first maturity	Males: 383 mm; Females: 417 mm
Age at first maturity	Males: 2.7 yrs; Females: 3 yrs
Significant difference in mean lengths	No; Males: 603 mm; Females: 614 mm
Significant difference in length frequencies	Yes (very small males absent)
Significant difference in age frequencies	Yes (very young males absent)
Sex ratio significantly different from 1:1	Yes (Males : Females - 1.34 : 1)
Occurrence of bisexuals	Many inactive bisexual fish, few transitional fish
Sexual pattern	Diandric protogynous hermaphroditism
Female length at 50% maturity	492 mm
Female age at 50% maturity	3.9 yrs
Spawning season	September to January
Non-spawning fish in the spawning season	Yes
Spawning along whole coast	No – not in southern region
Other north/south differences	No old fish in southern region; southern fish are larger than northern fish at the same age; more commonly caught in the northern region.
Growth curve	Logistic
L_∞	781mm
k	0.481 yr^{-1}
t_0	2.76 yrs
Time taken to attain 80% of L_∞	5.5 yrs
Z	0.684 yr^{-1}
M	0.416 yr^{-1}
F	0.268 yr^{-1}
t_c	2.9 yrs
Comparative mean lengths KZN/Mozambique	No data
Change in mean length (1980s vs 1990s)	Not significant; 551 mm vs 546 mm
SBPR at current F	42%
Change in F needed to attain $F_{0.1}$	Increase by 40%
Change in F needed to attain F_{SBR40}	Increase by 5%
Exploitation status	Optimally exploited
Mnimum size limit	400 mm
Recreational bag limit	5 $angler^{-1}day^{-1}$
Existing South African marine reserves	Possibly ineffective

It is possible that reproductively inactive fish migrate from south to north, evidenced by the general shortage of older fish in the southern area, although the limited tagging data do not support this. Even in the northern sampling region, numerous reproductively inactive large female fish were recorded during the spawning season. This suggests that some mature fish may not spawn every year.

At the same age, fish in the southern region were often larger than their counterparts in the northern region, suggesting faster growth. There was also a tendency for males to be larger than females at the same age, suggesting that males may grow faster than females, or that faster-growing fish become males. The differences were not sufficiently large enough to warrant separating the regions or sexes for the production of a growth curve. A logistic curve was chosen to describe growth, as it provided the best fit to the data. The combination of growth parameters, mortality rates, and the ages at maturity and first capture used here indicate that *E. andersoni* is currently optimally fished, with a spawning biomass per recruit level at 42% of the unfished level at the current fishing mortality. There is some support for this, as the mean length of catches of this species has remained unchanged since the mid-1980s.

Epinephelus rivulatus

A summary of the life history and other characteristics of this species is given in Table 6.2. *E. rivulatus* is widely distributed in the Indian Ocean and the western Pacific, ranging from the tropics to temperate latitudes. It is the second most common serranid recorded in commercial catches in the province of KwaZulu-Natal. It occurs at depths from the shore down to about 80 m, and is thus available to all sectors of the reef fishery viz. shore angling, spearfishing and recreational and commercial skiboat fishing. It is a small species, attaining a weight of about 1.5 kg. However, because of its small size, it is generally only retained by the commercial skiboat sector.

E. rivulatus demonstrates several of the characteristics typical of monandric protogynous hermaphrodites. There are bimodal length and age frequencies for the sexes, with an absence of small, young males and few large, old females; males mature at a larger size and at a greater age than females; the mean lengths of males and females are significantly different; and several mature females were recorded in the process of changing to males. An expected female-biased sex ratio was not found, possibly because the selectivity of the fishery resulted in smaller (female) fish being excluded from samples. *E. rivulatus* is therefore confirmed as being a monandric protogynous hermaphrodite. Female maturity is attained at a small size and early in the life of this species. Spawning was recorded over an extended period, during winter and spring. Very few large, reproductively inactive fish were found during the spawning season, and spawning was recorded along the whole coast of KwaZulu-Natal.

Fish in the southern region were often significantly larger than their counterparts in the northern region at the same age, suggesting faster growth. Males were often significantly larger than females at the same age, suggesting that males may grow faster, or that faster-growing fish become males. Von Bertalanffy growth curves provided the best fit to the data from both northern and southern sampling regions.

Table 6.2: Summary of life history and other characteristics of *E. rivulatus* established during this study. All lengths are TL. KZN = KwaZulu-Natal.

Distribution	Indian Ocean and western Pacific	
Biogeography	Tropical/subtropical	
Residency	Potentially high	
Catch methods	Skiboat fishing	
Local importance and value	Second most common serranid in commercial skiboat catches; low value (small size)	
Depth range	1 – 80 m	
Maximum length and age in this study	435 mm; 17 yrs	
Maximum weight in this study	1.2 kg	
Bimodal length/age frequency for sexes	Yes	
Length at first maturity	Males: 261 mm; Females: 165 mm	
Age at first maturity	Males: 3.1 yrs; Females: 1.3 yrs	
Significant difference in mean lengths	Yes; Males: 338 mm; Females: 298 mm	
Significant difference in length frequencies	Yes (very small males absent, few large females)	
Significant difference in age frequencies	Yes (very young males absent, few old females)	
Sex ratio significantly different from 1:1	Northern region only (Males : Females – 1.25 : 1)	
Occurrence of bisexuals	Few transitional fish	
Sexual pattern	Monandric protogynous hermaphrodite	
Female length at 50% maturity	219 mm	
Female age at 50% maturity	~ 2.1 yrs	
Spawning season	July to November	
Non-spawning fish in the spawning season	Very few	
Spawning along whole coast	Yes	
Other north/south differences	Southern fish are larger than northern fish at the same age; smaller fish caught in the northern area	
	Northern	Southern
Growth curve	Von Bertalanffy	Von Bertalanffy
L_∞	332 mm	366 mm
k	0.394 yr^{-1}	0.477 yr^{-1}
t_0	0.02 yrs	-0.41yrs
Time taken to attain 80% of L_∞	3.8 yrs	3.5 yrs
Z	1.121 yr^{-1}	1.14 yr^{-1}
M	0.68 yr^{-1}	0.803 yr^{-1}
F	0.375 yr^{-1}	0.276 yr^{-1}
t_c	4 yrs	4 yrs
Comparative mean lengths KZN/Mozambique	No data	
Change in mean length (1980s vs 1990s)	Yes; 281 mm vs 301 mm (significant)	
SBPR at current F	82%	87%
Change in F needed to attain $F_{0.1}$	Increase by 385%	Increase by 653%
Change in F needed to attain F_{SBR40}	Increase by 545%	Increase by 697%
Exploitation status	Lightly exploited	Lightly exploited
Mnimum size limit	None	
Recreational bag limit	5 $angler^{-1}day^{-1}$	
Existing South African marine reserves	Likely to be effective	

The combination of growth parameters, mortality rates, and the ages at maturity and first capture used here, indicate that *E. rivulatus* is currently only lightly exploited, based on a target spawning biomass per recruit level of 40% of the unfished level. There is support for this contention, since the mean length of this fish in skiboat catches has not decreased since the mid-1980s.

Epinephelus marginatus

A summary of the life history and other characteristics of this species is given in Table 6.3. *E. marginatus* is widely distributed around much of the African continent, except for the east African coast to the north of Mozambique, and appears to tolerate cool-temperate waters through to the tropics. It occurs at depths from the shore down to about 90 m, and is thus available to all sectors of the local reef fishery, namely shore angling, spearfishing and recreational and commercial skiboat fishing. It is a large species, attaining a weight of about 35 kg, and is particularly targeted by the skiboat sector because of its large size.

E. marginatus also has several characteristics that are typical of monandric protogynous hermaphrodites. There are bimodal length and age frequencies for the sexes, with an absence of small, young males and few large, old females; males mature at a larger size and at a greater age than females; the mean lengths of males and females are significantly different; and the sex ratio of the exploited population in KwaZulu-Natal is female-biased. Although no sex-changing fish were observed, the age data indicate that males can only be derived from females, and *E. marginatus* is confirmed as being a monandric protogynous hermaphrodite. Female maturity is attained at a large size and at a relatively old age. Spawning was recorded over an extended period, during spring and summer. Very few large, reproductively inactive fish were found during the spawning season, and spawning was recorded along the whole coast of KwaZulu-Natal.

Fish in the southern region were generally larger than their counterparts in the northern region at the same age, suggesting faster growth in the former region. Although very few males were recorded, they were larger than females at the same age, suggesting that the males may grow faster, or that faster-growing fish become males. A von Bertalanffy growth curve provided the best fit to the age/length data. The combination of growth parameters, mortality rates, and the ages at maturity and first capture used here indicate that *E. marginatus* is currently over-exploited, with a spawning biomass per recruit level at 33% of the unfished level at the current fishing mortality. This is supported by the reduction in mean length of catches of this species since the mid-1980s. Additionally, the mean length of fish caught in Mozambique, which had been exposed to low fishing effort at the time of sampling, was substantially larger than in KwaZulu-Natal. Furthermore, the sex ratio in samples from Mozambique was close to unity, suggesting that there had been no loss of large males from the population by fishing, as was observed in KwaZulu-Natal.

Table 6.3: Summary of life history and other characteristics of *E. marginatus* established during this study. All lengths are TL. KZN = KwaZulu-Natal.

Distribution	Southeast Africa, West Africa, Mediterranean
Biogeography	Tropical/subtropical/temperate
Residency	Potentially high
Catch methods	Skiboat fishing (mainly), spearfishing, shore angling
Local importance and value	High value
Depth range	1 – 140 m
Maximum length and age in this study	1 125 mm; 17 yrs (KZN); 24 yrs (Mozambique)
Maximum weight in this study	25.1 kg
Bimodal length/age frequency for sexes	Yes
Length at first maturity	KZN: Males: 800 mm; Females: 545 mm Mozambique:Males: 670 mm; Females: 560 mm
Age at first maturity (years)	KZN: Males: 10.5 yrs; Females: 5.1yrs
Significant difference in mean lengths	KZN: yes; Males: 917 mm; Females: 709 mm Mozambique: yes; Males: 785 mm; Females: 695 mm
Significant difference in length frequencies	KZN: yes; no small males and few large females Mozambique: yes; no small males, few large females
Significant difference in age frequencies	KZN: yes; no young males and few old females
Sex ratio significantly different from 1:1	KZN: yes (Males : Females – 0.18 : 1) Mozambique: no (Males : Females – 0.9 : 1)
Occurrence of bisexuals	One inactive bisexual; no transitional fish
Sexual pattern	Monandric protogynous hermaphrodite
Female length at 50% maturity	KZN: 624 mm; Mozambique: 580 mm
Female age at 50% maturity	KZN: 6.5 yrs
Spawning season	October to February
Non-spawning fish in the spawning season	Very few
Spawning along whole coast	Yes
Other north/south differences	Southern fish larger than northern fish at the same age; more commonly caught in the southern region
Growth curve	Von Bertalanffy
$L\infty$	1 070 mm
k	0.135 yr^{-1}
t_0	-2.66 yrs
Time taken to attain 80% of $L\infty$	12.3 yrs
Z	0.375 yr^{-1}
M	0.24 yr^{-1}
F	0.135 yr^{-1}
t_c	3 yrs
Change in mean length (1980s vs 1990s)	Yes; 660 mm vs 626 mm (not significant)
Comparative mean lengths KZN/Mozambique	626 mm vs 724 mm (significant)
SBPR at current F	33%
Change in F needed to attain $F_{0.1}$	Increase by 24%
Change in F needed to attain F_{SBR40}	Decrease by 19%
Exploitation status	Over-exploited
Mnimum size limit	400 mm
Recreational bag limit	5 $angler^{-1}day^{-1}$
Existing South African marine reserves	Effectiveness unknown

Epinephelus albomarginatus

A summary of the life history and other characteristics of this species is given in Table 6.4. *E. albomarginatus* is a subtropical species, and, being endemic to the east coast of South Africa and southern Mozambique, has a very restricted distribution. It occurs at depths from 30 m down to 120 m, and is thus only available to the skiboat sector of the local reef fishery. It is a medium-sized species, attaining a weight of about 13 kg.

E. albomarginatus has several features that are characteristically found in monandric protogynous hermaphrodites. There are bimodal length and age frequencies for the sexes, with an absence of small, young males and few large females; males mature at a larger size and a slightly greater age than females; the mean lengths of males and females are significantly different; and the sex ratio of the exploited population in KwaZulu-Natal is female-biased. Although no sex-changing (i.e. mature bisexual) fish were observed, the limited age data indicate that males are likely to be derived from mature females, and *E. albomarginatus* is probably a monandric protogynous hermaphrodite. Female maturity is attained at a large size and at a relatively old age, although the length at maturity of Mozambican females is much smaller than in KwaZulu-Natal. Very little reproductive activity was recorded in KwaZulu-Natal, even amongst large individuals during the spawning season, and mature fish were only found in the northern sampling region. This may be because this species is at the edge of its distributional range. The lack of larger, older fish in samples from the southern region suggests that there may be some migration from south to north. Spawning appears to occur over an extended period, during spring and summer.

E. albomarginatus in the southern region were generally larger than their counterparts in the northern region at the same age, suggesting faster growth. Few males were recorded, and some were larger than females at the same age, suggesting that the former sex may grow faster, or that faster-growing fish become males. A von Bertalanffy growth curve provided the best fit to the age/length data. The combination of growth parameters, mortality rates, and the ages at maturity and first capture used here indicate that *E. albomarginatus* in KwaZulu-Natal is currently over-exploited, with a spawning biomass per recruit level at 23% of the unfished level at the current fishing mortality. This is supported by the significant reduction in mean length of catches of this species since the mid-1980s. Moreover, the mean length of fish caught in Mozambique which had been exposed to low fishing effort at the time of sampling, was substantially larger than in KwaZulu-Natal, where effort was much higher.

Table 6.4: Summary of life history and other characteristics of *E. albomarginatus* established during this study. All lengths are TL. KZN = KwaZulu-Natal.

Distribution	Southeast African endemic
Biogeography	Subtropical
Residency	Unknown
Catch methods	Skiboat fishing
Local importance and value	Reasonably important; high value
Depth range	30 – 120 m
Maximum length and age in this study	870 mm; 15 yrs
Maximum weight in this study	11.1 kg
Bimodal length/age frequency for sexes	Yes
Length at first maturity	KZN: Males: 511 mm; Females: 600 mm Mozambique: Males: 591mm: Females: 329 mm
Age at first maturity (KZN)	Males: 7 yrs; Females: 6.8 yrs
Significant difference in mean lengths	KZN: not tested (too few fish) Mozambique: yes; Males: 746 mm; Females: 569 mm
Significant difference in length frequencies	KZN: yes; no small males and few large females Mozambique: yes; no small males, few large females
Significant difference in age frequencies	KZN: yes; no young males and few old females
Sex ratio significantly different from 1:1	KZN: not tested (too few fish) Mozambique: yes; Males : Females, 0.31 : 1
Occurrence of bisexuals	Few inactive bisexual fish
Sexual pattern	Monandric protogynous hermaphrodite
Female length at 50% maturity	KZN: 600 mm ; Mozambique: 341mm
Female age at 50% maturity	KZN: 6.8 yrs
Spawning season	October to February
Non-spawning fish in the spawning season	Most KZN fish were reproductively inactive
Spawning along whole coast	Very little spawning recorded, only in northern area
Other north/south differences	Southern fish larger than northern fish at the same age; no old fish in the southern region
Growth curve	Von Bertalanffy
L_∞	789 mm
k	0.214 yr^{-1}
t_0	0.09 yrs
Time taken to attain 80% of L_∞	7.6 yrs
Z	0.468 yr^{-1}
M	0.228 yr^{-1}
F	0.224 yr^{-1}
t_c	3.4 yrs
Change in mean length (1980s vs 1990s)	Yes; 588 mm vs 557 mm (significant)
Comparative mean lengths KZN/Mozambique	557 mm vs 640 mm (significant)
SBPR at current F	23%
Change in F needed to attain $F_{0.1}$	Decrease by 7%
Change in F needed to attain F_{SBR40}	Decrease by 43%
Exploitation status	Over-exploited
Mnimum size limit	400 mm
Recreational bag limit	5 $angler^{-1}day^{-1}$
Existing South African marine reserves	Effectiveness unknown

Comparative summary of life histories, and implications for harvesting

The various life history characteristics of the four species and the implications for harvesting can be broadly discussed in terms of three categories: distributional aspects, reproductive aspects and growth and mortality aspects. These will be presented here, followed by a summary of the relative vulnerabilities of these species to harvesting.

Distribution

Two of the species investigated here, *E. andersoni* and *E. albomarginatus*, have very limited biogeographical distributions, while *E. rivulatus* and *E. marginatus* are far more widely distributed. The implication of this, from a fisheries perspective, is that there is less likelihood of stocks being replaced by immigration in the event of localised depletion. Regarding cross-shelf distribution, three of the species occur in shallow water depths, which means they are vulnerable to exploitation from all fishery sectors. *E. albomarginatus* only occurs in depths >30m, and is therefore only accessible to the skiboat fishery. The fast-flowing Agulhas current often prevents effective fishing in these deeper waters, hence this species theoretically enjoys greater protection from exploitation. Little is known about the residency of these four species, although limited tagging evidence suggests that *E. andersoni* and *E. marginatus* are resident (Appendix 2), and hence are more vulnerable to local depletion where fishing occurs. This may also apply to *E. rivulatus* (Mackie, 1998).

Reproduction

Within the reproductive aspects of life histories, three interlinked features can be identified: Sex change, length/age at maturity and spawning patterns.

Sex change

As a preliminary proviso, it needs to be noted that there are difficulties in assessing the full implications of protogyny for these four species, since they have been subjected to fishing for many years. Three of the four species investigated here are monandric protogynous hermaphrodites (*E. rivulatus*, *E. marginatus* and *E. albomarginatus*), while *E. andersoni* is a diandric protogynous hermaphrodite. In the absence of fishing, the reproductive output of protogynous species may be greater than in gonochorists, but, unless reproductive success remains high, the converse is likely to apply when fishing occurs (Bannerot *et al.*, 1987; Buxton, 1993).

In *E. andersoni*, because the numbers, lengths and ages of males and females are equivalent over the exploited size range, males and females are equally likely to be caught. In *E. marginatus* and *E. albomarginatus*, however, males are less numerous, and larger and older than females. While their lower numbers means that males are less likely to be caught, they are potentially more vulnerable to capture because of their larger size, as fishers target larger fish. Differential capture of males in protogynous species has resulted in a substantial reduction in the numbers of this sex e.g. in the sparids *Chrysoblephus cristiceps* and *C. puniceus* in South Africa (Buxton, 1993; Garratt, 1993) and the serranids *E. striatus* and *Mycteroperca venosa* from the Caribbean (Thompson and Munro, 1983) and *M.*

microlepis from the U.S. south Atlantic (McGovern *et al.*, 1998). It is also possible that some aspect of male behaviour, such as aggression, means they are more liable to be caught than females (Gilmore and Jones, 1992). *E. marginatus* males, for example, are reported to be more active and aggressive than females (Zabala *et al.*, 1997a, 1997b), and are therefore more likely to encounter baited hooks. At the commencement of fishing, initial losses of males in these species may initially be of little consequence (assuming parity in sex ratio), but as numbers of males decline, loss of males assumes increasing significance. For *E. rivulatus*, the potential effects of fishing are not as clear, because the small size of this species means that much of the stock is not available to the fishery. This is particularly the case in the recreational fishery, where very few of these fish are retained as they are not considered worth keeping.

The implications of a differential loss of males in a protogynous species is that low numbers of males may limit reproductive success i.e. there is sperm limitation (Bannerot *et al.*, 1987). Unless the species possesses the ability to compensate for this, for example, by reducing the age at sex change, or by increasing the rate of female to male sex change, reproductive success may be compromised (Bannerot *et al.*, 1987; Huntsman and Schaaf, 1994). Few published studies support the existence of compensatory mechanisms to reduce sperm limitation in serranids. Ferreira and Russ (1995) showed that greater numbers of transitional and small male *Plectropomus leopardus* occurred on fished reefs compared to unfished reefs in Australia. This suggests that the rate of sex change had increased in response to the removal of larger males by fishing. Fishing has also resulted in a reduction in size at sex change and a female-biased sex ratio in the protogynous *Mycteroperca microlepis* and *M. phenax* from the Gulf of Mexico (Coleman *et al.*, 1996). These authors suggested that the ability of a species to compensate was governed by its behaviour. For example, in a species that remains in contact with conspecifics throughout the year, assessments as to whether to change sex can be made at any time, whereas those that only aggregate at limited times can only make these assessments then (Shapiro *et al.*, 1993a). Coleman *et al.* (1996) suggest that, in the protogynous serranid, *E. guttatus*, which has shown no change in sex ratio over many years of fishing (Shapiro *et al.*, 1993b), regular contact between individuals has enabled compensatory sex change to maintain a stable sex ratio. Thus, fishing is less likely to alter sex ratios in this case (Coleman *et al.*, 1996). In a related argument, Koenig *et al.* (1996) recently discussed the possibility that fishing may have actually negated some of the sperm-limitation mechanisms initially induced by fishing, namely, if greater numbers of sex-changing individuals occurred as a result of fishing, these fish could also be selectively removed, as they assume male characteristics even before the sex-change process is completed (Shapiro, 1987).

In this study, there is only limited evidence to suggest that the species can respond to a sperm-limiting situation induced by fishing. The variable size at sex change in these species suggests that the process is socially mediated (Shapiro, 1987), so at least the potential to respond exists. For *E. albomarginatus*, it is possible that the timing of the onset of sex change has changed in response to fishing. The smallest male sampled in KwaZulu-Natal waters was 511 mm (TL), while in Mozambican samples, exposed to less fishing pressure, the smallest male was 591 mm (TL). This may indicate a response by this species to reduce the size at sex change in

KwaZulu-Natal area. Clearer interpretation of these results is difficult, as very few males were sampled, perhaps because this species is at the edge of its distributional range, or because the stock in KwaZulu-Natal has been heavily fished.

A smaller size at maturity in male *E. marginatus* from KwaZulu-Natal compared to males from Mozambique was not apparent, although numbers of samples were also very low. The sex ratio in the more heavily fished area, however, was strongly female-biased relative to that in the lightly fished area. This species apparently only forms groups during the spawning season (Zabala *et al.*, 1997a, 1997b), which supports predictions that the sex ratio of protogynous species, in which individuals spend limited time together, may be skewed as a result of fishing (Coleman *et al.*, 1996). Caution is required, however, in attributing changes in sex ratios to fishing, as spatial segregation by sex may confound the interpretation of observed ratios in catches (Jennings and Lock, 1996). There are no comparative data from unfished areas for *E. rivulatus*. An expected female-biased sex ratio, typical of monandric protogynous species, was not observed in this species, although, owing to its small size, much of the population is currently not available to the fishery. In Western Australia, this species lives in loose associations throughout the year (Mackie, 1998), which would therefore allow continuous assessment of existing sex ratios, and hence fishing may not result in a biased sex ratio.

Anecdotal reports and personal observations suggest that *E. andersoni* is also a gregarious species, hence there are potentially many encounters during which assessments on whether to become a male or not may be made. As in *E. rivulatus*, this may account for the observed the male-biased sex ratio of the exploited population. Being diandric, some mature females do undergo sex change, and it is possible that because of fishing, there are insufficient males derived by this route to ensure that spawning can occur. An increased rate of immature female to male development may have arisen in order to compensate, resulting in the observed large numbers of small, inactive bisexuals and small, young males. This may be a similar situation to that observed in *P. leopardus* (Ferreira and Russ, 1995), but in the absence of information on the age and sex structure of an unfished population of *E. andersoni*, this suggestion is speculative. Also speculative, fish with a genetic disposition to change sex may have been selectively removed by fishing (owing to their larger size), hence there has been genetic selection for fish which become male early in their lives, leading to the observed numbers of small males and inactive bisexual fish. No literature could be found to support this suggestion.

Length and age at maturity

The earlier in life that a fish matures, the earlier it will be able to reproduce, and the longer will be the period during its lifespan over which it can reproduce. Early maturation implies that there are larger numbers of fish available to spawn, as later-maturing fishes potentially experience greater opportunity for losses due to natural mortality and fishing mortality before they mature. Both *E. andersoni* and *E. rivulatus* mature at relatively small sizes and young ages, while *E. marginatus* and *E. albomarginatus* mature at substantially greater lengths and ages. For *E. albomarginatus*, estimation of these parameters for the KwaZulu-Natal population was problematic, as this area constitutes the edge of its distributional range, and few mature fish were sampled. For both *E. marginatus* and *E. albomarginatus*,

though, late maturity means that these species should only be harvested later in their lives.

Fishing is able to cause changes in the length at maturity. For example, the length at maturity of female *M. microlepis* in the south-eastern United States was reduced by heavy fishing pressure over a 15 to 20 year period (Coleman *et al.*, 1996; McGovern *et al.*, 1998). Testing for this effect requires a long-term data set on maturity, or access to information on maturity collected in an unexploited area. No long-term maturity data are available for the species investigated here, while the comparative maturity data from heavily fished and lightly fished areas produced equivocal evidence for *E. marginatus* and *E. albomarginatus*. The length at maturity of female *E. marginatus* was not significantly lower in KwaZulu-Natal than in Mozambique, where fishing pressure was light at time of sampling. For *E. albomarginatus*, length at maturity in females was much smaller in Mozambique, although this may be because KwaZulu-Natal is at the end of the distributional range of this species, resulting in atypical estimates of maturity in the latter area. Although reduction in size at maturity is ostensibly a positive result, since continued spawning is possible despite an overall reduction in mean size, these smaller fish are likely to be less fecund (Bohnsack, 1990) and hence, total reproductive output may be reduced.

Spawning patterns

Three aspects of spawning could affect exploitation status, namely spatial, temporal and qualitative aspects. Regarding spatial spawning patterns, the two endemic species, *E. andersoni* and *E. albomarginatus*, showed little or no evidence of spawning in the southern sampling area, perhaps because they are at the southern limit of their distributional range in KwaZulu-Natal. This may imply that their reproductive output in KwaZulu-Natal is reduced relative to *E. rivulatus* and *E. marginatus*, in which spawning was recorded along the whole coast. It is also possible that the southern populations of the former two species are being maintained by ocean current-assisted larval recruitment from the north (Beckley, 1993), a similar situation to that suggested for another endemic species, the sparid *Chrysoblephus puniceus* (Garratt, 1993). In parts of the Caribbean, where there is an absence of spawning adults, the reef fishery is also thought to be maintained by recruitment from a distance (Munro, 1983). Also, in parts of the Mediterranean, catches of *E. marginatus* are made in areas where no spawning occurs (Chauvét, 1991). These observations are suggestive of a source-sink scenario (Crowder *et al.*, 2000) i.e. in which one area is a net exporter of individuals and another area is a net importer (Pulliam, 1988). Thus, for *E. andersoni* and *E. albomarginatus* in KwaZulu-Natal, the northern populations could be functioning as a source of recruits for the southern "sink" population, mediated by south-flowing currents. If, however, there is also migration of mature-sized adults from the south to the north, as suggested in Chapter 4, the source-sink theory is not as clear.

There are some indications that *E. andersoni* may form aggregations related to spawning, although the evidence is circumstantial. Unusually large catches of this species are occasionally made during or around the spawning season, but, based on reports by fishers, these do not appear to occur in very localised areas. This does not preclude the possibility that they are spawning aggregations, though, as

aggregations may not consistently occur in the same area each year (Shapiro *et al.*, 1993a), and spawning aggregations on a large spatial scale are known for other serranids (Domeier and Colin, 1997). Increased catches of *E. andersoni* are regularly reported from the southern sampling area during the winter, and, also from the southern sampling area, there has been one observation of a large group of individuals (*circa* 100) swimming rapidly over sand i.e. not in the vicinity of any reefs. Together with the absence of old (>6 years) fish in this area, this suggests that reproductively inactive fish may aggregate in the southern region prior to the spawning season, and then migrate northwards to join the spawning component of the population. Aggregated spawning may occur over a large area and over an extended period. Based on the data obtained in this study, there are no indications that the other three species form spawning aggregations in KwaZulu-Natal. However, *E. marginatus* is reported to form small, localised spawning aggregations in the Mediterranean (Zabala *et al.,* 1997a, 1997b). The significance of spatially localised aggregations from a harvesting perspective is that, if their locality is known to fishers, they enable massive short-term catches, with considerable disruption of the spawning process, and consequent impacts on recruitment and future yield (Domeier and Colin, 1997; Garratt, 1996).

Investigation of temporal spawning patterns showed that all four species investigated here have extended spawning seasons, unlike some serranids which spawn over a very short period e.g. *E. striatus* and *E. guttatus* in the western Atlantic (Colin, 1992; Shapiro *et al.*, 1993a). Spawning over a longer period reduces the risk of disruption of the spawning process by fishers, assuming that spawning occurs in a localised area and that the location of the area is known to the fishers. Apart from *E. rivulatus*, the species investigated here spawn in spring and summer. The disruptive effects of fishing on spawning may be reduced in *E. rivulatus*, since it spawns during months when weather conditions often prevent fishing taking place.

An apparent lack of reproductive activity in large females during the spawning season was recorded in all four species, but particularly in *E. andersoni*. Coleman *et al.* (1996) suggested that non-spawning in female *M. microlepis* was a response to a shortage of males. Although this argument may apply to *E. marginatus* and *E. albomarginatus*, it is not valid for *E. andersoni* and *E. rivulatus*, in which males outnumbered females. No other published examples of non-spawning in mature-sized fishes could be found, apart from in the sparid *Acanthopagrus australis* from Australia. In this species, there was an increasing tendency for older females not to participate in spawning migrations, although these fish produced vitellogenic eggs (Pollock, 1984). This author speculated that these fish had not accumulated sufficient energy reserves to migrate and spawn. It is possible that some of the large *E. andersoni* could have insufficient resources for successful spawning, and therefore remain in a reproductively inactive state. Alternatively, there may be social factors that cause some females not to spawn in a particular year. The significance of these fish that apparently do not spawn every year may not be known, but the likely effect is a reduction in overall reproductive output.

Finally, it is likely that larger individuals make a disproportionately large contribution to reproductive output, since they are more fecund and hence capable of producing more sperm or eggs. Since fishing results in the removal of larger individuals, their

loss results in relatively lower output than a population in which larger individuals are common. The relative contribution to reproductive output by larger fish is not known, but assuming it is substantial (e.g. Collins *et al.*, 1998), losses of these fish will negatively affect reproductive success and recruitment (Bohnsack, 1990).

Growth and mortality

The growth rates of the four species investigated here differ markedly. *E. rivulatus* attains 80% of its L∞ in about 3.5 years, *E. andersoni* attains 80% of L∞ in 5.5 years), *E. albomarginatus* attains 80% of L∞ in 7.6 years and *E. marginatus* attains 80% of L∞ in 12.3 years. Slow growth implies a longer period before maturation, and hence a larger window of opportunities for capture before spawning. Slower-growing species are therefore more vulnerable to recruitment over-fishing if a minimum size limit is not imposed.

Closely correlated with growth rate are maximum size, longevity and natural mortality. With the exception of *E. rivulatus*, the species investigated here attain large maximum sizes, particularly *E. marginatus* (Tables 6.1 - 6.4). All four species are relatively long-lived, from 11 years (*E. andersoni*) to 17 years (*E. rivulatus*). It should be noted that these age estimates are for fish from exploited populations, and, hence, probably under-estimate longevity (Huntsman *et al.*, 1999). It is therefore perhaps more than coincidental that the oldest age estimate is from an under-exploited species. Greater longevity can be advantageous from a fisheries perspective, though, as it acts as a buffer against recruitment variability that affects harvesting of short-lived species such as sardines (Armstrong and Thomas, 1989). Again with the exception of *E. rivulatus*, natural mortality estimates for these species are low, particularly for *E. marginatus* and *E. albomarginatus*. Species experiencing low natural mortality have low rates of population turnover, and therefore reduced productive capacity (Gulland, 1971).

Much theoretical work has been undertaken to demonstrate the potential relationship between natural mortality (M) and the optimum level of fishing mortality (F). Gulland (1971) proposed that F/M = 1 would be optimal, while Francis (1974) and others suggested a range of F/M values of between 0.8 and 1.5. An F/M ratio of 1 has been suggested for as a reference point for many years (e.g. Pauly, 1983; Clark, 1991). More recently, there have been suggestions that optimal values of F are much lower than this. Walters and Pearse (1996), for example, indicate that an F/M value of <0.66 may be more appropriate, and, for species with very low M values, suggest that as little as 10% of the biomass should be harvested each year. The low M values for *E. marginatus* and *E. albomarginatus* estimated in this study therefore suggest that these species may be particularly vulnerable to exploitation.

Relative vulnerabilities to harvesting

The preceding discussion on these life history characteristics, and their relevance to the vulnerability of the four species to harvesting, is summarised in Table 6.5 using a simple scoring system. Note that a positive score does not necessarily indicate that the life history feature is of absolute benefit to the species, but may have been allocated because it infers some benefit to that species relative to the others. For

the sake of simplicity, no weighting of any features has been attempted, although some have more significance from a fisheries perspective.

The table permits a simple assessment of the vulnerability of these species to harvesting. *E. marginatus* and *E. albomarginatus* both have many negative values, while *E. andersoni* and particularly *E. rivulatus* have fewer. This is reflected in the current exploitation status of the species, with *E. marginatus* and *E. albomarginatus* being over-exploited in KwaZulu-Natal, while *E. andersoni* is currently optimally exploited, and *E. rivulatus* is under-exploited. *E. marginatus* and *E. albomarginatus* are "typical" serranids, exhibiting monandric protogynous hermaphroditism, slow growth and large maximum sizes. *E. andersoni* and *E. rivulatus*, however, are atypical serranids, being particularly distinguished by a diandric protogynous hermaphroditic reproductive style and relatively fast growth in the former species, and a combination of fast growth, small size and early maturity in the latter.

Table 6.5: Summary of life history features for four serranids from KwaZulu-Natal, and implications for vulnerability to harvesting. A plus sign (+) indicates a feature which potentially confers resilience to harvesting, a minus (-) indicates a negative feature. A question mark ? indicates uncertainty.

	E. andersoni	*E. rivulatus*	*E. marginatus*	*E. albomarginatus*
Distributional range	-	+	+	-
Residency	-	-	-	?
Depth range/catchability	-	-	-	+
Caught by all fishery sectors	-	+	-	+
High market value	-	+	-	-
Female size/age at maturity	+	+	-	-
Male size/age at maturity	+	-	-	-
Fewer males than females	+	+	-	-
Regular assessment of sex ratio	+	+	-	-
Males larger than females	+	-	-	-
Diandry	+	-	-	-
Non-spawning by some fish	-	+	+	-
Extended spawning season	+	+	+	+
Spawns throughout range	-	+	+	-
Spawns when fishing effort is low	-	+	-	-
Spawns in aggregations	-	+	-	?
Growth rate	+	+	-	-
Large size	-	+	-	-
Longevity	-	-	-	-
Low natural mortality	+	+	-	-
Relative age at first capture	-	+	-	-
Harvest refugia	?	+	?	?

Many other South African reef fishes, particularly members of the family Sparidae, are considered to be over-exploited (Griffiths, 1997b; Mann, 2000). Sparids share some of the life history characteristics of serranids, notably complex life histories and slow growth. Of all the South African sparid species that are targeted by the linefishery that have been investigated to date, only two are not considered to be over-exploited. Significantly, one of these, *Sarpa salpa*, is small, fast-growing, and short-lived (van der Walt and Govender, 1996), while the other, *Rhabdosargus sarba*, is difficult to target because it is not reef-associated (Mann and Radebe, 2000).

This trend in the over-exploitation of reef fish species is also found in the Gulf of Mexico and the Caribbean, where all reef fish stocks whose status is known are over-fished (Coleman *et al.*, 1999). The reef fishery there is largely based on serranids and snappers (Lutjanidae), most of which also have life history styles that make them vulnerable to fishing. In a recent review of reef fishes in the area, several investigators documented dramatic declines in catches, mean sizes and numbers of males in several species (Huntsman *et al.*, 1999; Coleman *et al.*, 1999). Despite historical warnings that over-fishing of the Gulf of Mexico and Caribbean species was likely to occur (Huntsman, 1983), stocks of these species have declined. Around the world, other fisheries based on reef fishes have also evidenced serious declines (reviewed in Jennings and Lock, 1996).

Fisheries management

Current management

How, then, are increasing human demands for the flesh of reef fishes to be reconciled with their often complex life histories? In theory, fisheries management should address this dilemma. The approach to the management of reef fishes in South Africa has mirrored that elsewhere, and a brief summary of the measures adopted for *E. andersoni*, *E. rivulatus*, *E. marginatus* and *E. albomarginatus* is presented here. Thereafter, some comments will be made on the effectiveness of these measures.

For most of the 20th century, there was no management of the reef fishery in South Africa. In the province of KwaZulu-Natal, a minimum size limit of 300 mm (TL) was introduced in 1974 for *E. andersoni* and *E. marginatus* caught from the shore. On a national basis, the same limit was introduced for the skiboat sector and for *E. albomarginatus* in 1984. The size limit for these species was subsequently raised to 400 mm (TL) for all fishery sectors in 1991. For *E. andersoni* and *E. marginatus*, a daily bag limit for recreational shore anglers of five fish was also introduced in 1974 in KwaZulu-Natal. In 1984, the same bag limit was introduced on a national basis for the skiboat sector and for *E. albomarginatus*. An equivalent bag limit for *E. rivulatus* was subsequently introduced in 1992. The bag limit for recreational fishers is more restricting than it appears, since serranids belong to a regulatory category of which not more than five of any one species, or more than five in total from this category, may be kept per day. In addition to these measures, there is a large marine protected area, comprising the St Lucia marine reserve (established in 1979), and the adjacent Maputaland marine reserve (established in 1986). Located to the north of the northern sampling area, this protected area has theoretically provided a harvesting refuge from skiboat catches of these species. None of these management measures were based on hard science, but were an attempt to ensure sustainability of harvesting using the best available knowledge.

The effectiveness of a minimum size limit depends on the appropriateness of the size limit i.e. whether it is sufficiently large to allow a reasonable proportion (usually 50 %) of the population to spawn before harvesting. Its effectiveness also relies on compliance with the regulation, and on the survival of released, under-sized fishes (Waters and Huntsman, 1986). The current size limits for *E. andersoni*, *E.*

marginatus and *E. albomarginatus* are all below the female sizes at 50% maturity for these species (Tables 6.1, 6.2, 6.3). The disparity between the two parameters is particularly large for *E. albomarginatus*, although the size at maturity for this species could only be roughly estimated in KwaZulu-Natal. These size limits have had a deleterious effect on stocks of these three species, by permitting their capture before these fish have matured. Additionally, the current minimum size limits for the monandric protogynous species (*E. marginatus* and *E. albomarginatus*) are much lower than the minimum size of males, hence affording this sex no protection at all.

Owing to the vigilance of local conservation officials, compliance with bag and size limits is probably met in the skiboat sector (which catches most of the serranids) on most fishing outings (pers. obs.). Survival of released fishes depends on the manner on which they are treated after they have taken the bait. If they are brought rapidly to the surface, the incidence of barotrauma is increased (pers. obs.), and hence post-release survival is reduced. There is also an increased incidence of barotrauma and reduced survival of released fishes as capture depth increases (Wilson and Burns, 1996; pers. obs.), and commercial skippers in KwaZulu-Natal believe that survival of released serranids caught at depths greater than 30 m is low (Appendix 1). However, recaptures of tagged *E. andersoni* and *E. marginatus* caught at depths >20 m indicate that there is at least some survival of these species post-release (Appendix 2; Chris Wilke, Marine and Coastal Management, PBX2, Roggebaai, 8012, South Africa, pers. comm.). Although difficult to quantify, the minimum size limit of 400 mm may therefore only have provided some benefit to *E. andersoni*, *E. marginatus* and *E. rivulatus*, as small specimens of these species live in shallow waters (Chapter 2). *E. albomarginatus*, however, only occurs in water depths >30 m, and survival following capture is therefore unlikely.

Recreational fishers in KwaZulu-Natal rarely attain their bag limits (Sauer *et al.* 1997a; Mann *et al.* 1997), and almost never in the case of serranids (Fennessy and Radebe, 2000), because the limits are higher than what the fishers are able to catch. The effect of this management measure, although difficult to quantify, is therefore unlikely to have been very effective.

The St Lucia and Maputaland marine reserves were established in order to provide protection for nesting turtles, coral reefs and the coral-associated communities occurring there. Diving and fishing surveys have shown that the fishes found there are mostly typical coral reef species (Chater *et al.*, 1993; Chater *et al.*, 1995), and only one of the serranids investigated in this study, *E. rivulatus*, appears to occur in any abundance. Although the surveys were not comprehensive, inspections of illegal catches of reef fish from the area also reveal very few individuals of *E. andersoni*, *E. marginatus* or *E. albomarginatus* (Fennessy, unpubl. data). It appears, therefore, that the existing marine reserves in KwaZulu-Natal may not constitute a substantial harvesting refuge for these serranids, although surveys in deeper water in the reserves may show otherwise.

Future management scenarios

It appears, then, that the current management measures for these four serranids have probably only had limited success in maintaining the viability of their stocks.

Recently, the emphasis in management of South African reef fishes has shifted towards the adoption of operational management procedures, ideally based on reference points derived from per recruit analyses (Griffiths, 1997). As already discussed (Chapter 5), these models fail to address many aspects of the life history of fishes, and hence, are often inadequate (Vincent and Sadovy, 1998). This is not surprising, as the life history processes themselves are not well understood by biologists and ecologists, let alone the modelers and managers. These processes also vary substantially in their manifestation from species to species, and from one stock to the next. In the words of Johannes (1998): "Nature is too complex and too variable". The data requirements in order to determine the input parameters to the models are also enormous. Even standard per recruit analyses, as undertaken in this study, have considerable data requirements. Reef fisheries are rarely based on a single species, hence fishery management measures need to be based on assessments of all the individual species that feature in the fishery – a daunting and unlikely scenario.

Summary tables similar to Table 6.5 may assist in the identification of species that are particularly vulnerable. For some species, the tables will be incomplete, and there may be debate about whether a particular feature of a species should be assigned a positive or a negative value. For most species, though, the table will be virtually empty, and by the time it is complete, the species could have been extirpated. A simpler assessment, proposed by Jennings *et al.* (1999), relies on identifying species that are potentially vulnerable to over-fishing, by comparing changes in abundance of their phylogenetic relatives as a function of maximum size. Assessments can be simpler still, such as the "data-less" management approach suggested by Johannes (1998). Assessment tables can also be more inclusive, when they are intended for fisheries rather than species, such as those of Pitcher *et al.* (1998). These authors chose a range of attributes for a variety of fisheries, incorporating ecological, technological, economic and social categories, and ranked the fisheries based on their multidisciplinary "health".

These types of assessments can assist in making decisions on how best to manage species and fisheries. The ultimate goal, though, is to manage ecosystems, or we may find ourselves harvesting species and managing fisheries that are very low down on the trophic scale (Pitcher and Pauly, 1998). The tools required for such ecosystem management are still inadequate. While they are being developed, though, fishing continues. In the interim, it is important to conserve at least parts of the various ecosystems in which harvested species live. Marine reserves not only conserve species, they conserve ecosystems and genetic biodiversity too (Bohnsack, 1993; 1996). They are also potentially valuable from a fisheries perspective, as they can seed adjacent exploited areas (Marine Reserves Task Group, 1997; Walters, 1998). As described above, the existing marine reserves in KwaZulu-Natal do not appear to protect either the serranids investigated in this dissertation, or their habitat. These protected areas do appear to fulfil this role for an endemic, protogynous sparid, *C. puniceus*, that is also targeted by the hook and line fishery, and it has been suggested that these areas have been partly responsible for sustaining the fishery for this species (Garratt, 1993). A system of no-take marine reserves, located in appropriate areas, may therefore also be influential in the conservation of serranids of the genus *Epinephelus* in KwaZulu-Natal.

REFERENCES

Abu-Hakima, R. 1987. Aspects of the reproductive biology of the grouper, *Epinephelus tauvina* (Forskal), in Kuwaiti waters. *Journal of fish biology.* **30**: 213-222.

Adams, P.B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fishery bulletin.* **78**: 1-12.

Anderson, R.C., Waheed, Z., Rasheed, M. and Arif, A. 1991. Reef fish resources survey in the Maldives - Phase 2. Bay of Bengal Programme, Madras, BOBP/WP/80, MDV/88/007. 51 pp.

Appeldoorn, R.S. 1996. Model and method in reef fishery assessment. *In: Reef fisheries.* Polunin, N.V.C and Roberts, C.M. Eds. Chapman and Hall, London. pp. 219-248.

Armstrong, M.J. and Thomas, R.M. 1989. Clupeiods. In: *Oceans of life.* Payne, A.I.L. and Crawford, R.J.M. Eds. Vlaeberg Publishers, Cape Town. pp. 105-121.

Atz, J.W. 1964. Intersexuality in fishes. In: *Intersexuality in vertebrates including man.* Armstrong, C.N. and Marshall, A.J. Eds. New York Academic Press: pp. 145-232.

Bannerot, S.P. 1984. The dynamics of exploited groupers (Serranidae): An investigation of the protogynous hermaphroditic reproductive strategy. PhD thesis. University of Miami. 393

Bannerot, S.P., Fox, W.W. and Powers, J.E. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. In: *Tropical snappers and groupers: Biology and fisheries Management.* Polovina, J.J. and Ralston, S. Eds. Westview Press, Inc., Colorado. pp. 561-605.

Beamish, R.J. and Fournier, D.A. 1981. A method for comparing the precision of a set of age determinations. *Canadian journal of fisheries and aquatic sciences.* **38**: 982-983 pp.

Beckley, L.E. 1985. The fish community of East Cape tidal pools and an assessment of the nursery function of this habitat. *South African journal of zoology.* **20**: 21-27.

Beckley, L.E. 1993. Linefish larvae and the Agulhas Current. In: *Fish, fishers and fisheries. Proceedings of the second South African marine linefish symposium.* Beckley, L.E. and van der Elst R.P. Eds. Durban, 23-24 October 1992. Special Publication, Oceanographic Research Institute. **2**: 57-63.

Beckley, L.E. 2000. Species composition and recruitment of tidal pool fishes in KwaZulu-Natal, South Africa. *African Zoology.* **35(1)**: 29-34.

Beckley, L.E. and van Ballegooyen, R.C. 1992. Oceanographic conditions during three ichthyoplankton surveys of the Agulhas current in 1990/1991. *South African journal of marine science*. **12**: 83-93.

Bennett, B.A. 1988. Some considerations for the management in South Africa of galjoen *Coracinus capensis* (Cuvier), an important shore-angling species off the south-western cape. *South African journal of marine science.* **6**: 133-142.

Beverton, R.J.H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapport et proces-verbaux des reunions. Conseil international pour l'Exploration de la Mer.* **154**: 44-67.

Beverton, R.J.H. and Holt, S.J. 1956. A review of methods for estimating mortality rates in fish populations, with special references to sources of bias in catch sampling. *Rapport et proces-verbaux des reunions. Conseil international pour l'Exploration de la Mer.* **140**: 67-83.

Beverton, R.J.H. and Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fishery Investigations Ministry of Agriculture, Fisheries and Food. Great Britian. Series 2.* **19**: 533 pp.

Beverton, R.J.H. and Holt, S.J. 1959. A review of the lifespan and mortality rates in nature and their relation to growth and other physiological characteristics. *Ciba Foundation. Colloquia on ageing.* **5**: 142-180.

Bohnsack, J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. South Atlantic. *NOAA technical memorandum NMFS SEFC.* **216**: 45 pp.

Bohnsack, J.A. 1993. Marine reserves. They enhance fisheries, reduce conflicts, and protect resources. *Oceanus.* **36**: 63-71.

Bohnsack, J.A. 1996. Marine reserves, zoning and the future of fishery management. *Fisheries.* **21(9)**: 14-16.

Booth, A.J. and Buxton, C.D. 1997. The management of the panga *Pterogymnus laniarius* (Pisces: Sparidae) on the Agulhas Bank, South Africa using per-recruit models. *Fisheries research.* **32**: 1-11.

Bouáin, A. 1984. Contribution à l'étude de Serranidés des côtes tunisiennes. Thèse dr. Etat, Univ. Tunis: 93 pp. Reported in Bouchereau *et al.*, 1999.

Bouáin, A. 1985. Croissance linéaire des mérous du Golfe de Gabès (Tunisie). *Rapport et proces-verbaux des reunions. Conseil international pour l'Exploration de la Mer.* **29(8)**: 99-100

Bouáin, A. and Siau, Y. 1983. Observations on the female reproductive cycle and fecundity of three species of groupers (*Epinephelus*) from the southeast Tunisian seashores. *Marine biology.* **73**: 211-220.

Bouchereau, J.L., Body, P. and Chauvét, C. 1999. Growth of dusky grouper *Epinephelus marginatus* (Linnaeus, 1758)(Teleostei, Serranidae) in the Natural Marine Reserve of Lavezzi Islands, Corsica, France. *Scientia marina.* **63(1)**: 71-77.

Brulé, T. and Deniel, C. 1996. Biological research on the red grouper (*Epinephelus morio*) from the southern Gulf of Mexico. In: *Proceedings of an EPOMEX/ICLARM international workshop on tropical snappers and groupers.* Arreguin-Sanchez, J. Munro, M.C. Balgos and D. Pauly. Eds. 26-29 October 1993, Campeche, Mexico. pp. 28-42.

Brulé, T., Deniel, C., Colas-Marrufo, T. and Sanchez-Crespo, M. 1999. Red grouper reproduction in the southern Gulf of Mexico. *Transactions of the American Fisheries Society.* 128: 385-402.

Brulé, T., Colas-Marrufo, T., Tuz-Sulub, A. and Deniél, C. 2000. Evidence for protogynous hermaphroditism in the serranid fish *Epinephelus drummondhayi* (Perciformes: Serranidae) from the Campeche Bank in the southern Gulf of Mexico. *Bulletin of marine science.* **66(2)**: 513-521.

Bruslé, J. 1985. Expose synoptique des données biologiques sur les merous *Epinephelus aeneus* (Geoffroy St Hilaire, 1809) et *Epinephelus guaza* (Linnaeus, 1758) de l'ocean Atlantique et de la Mediterranée. *FAO, synopsis sur les peches.* **129**: 64 pp.

Bruslé, J. and S. Bruslé. 1975. Ovarian and testicular intersexuality in two protogynous Mediterranean groupers, *Epinephelus aeneus* and *Epinephelus guaza*. In: *Intersexuality in the animal kingdom.* Reinboth, R. Ed. Springer-Verlag, New York. pp. 222-227.

Bruslé, J. and S. Bruslé. 1976. Contribution a l'etude de la reproduction de deux especes de merous (*Epinephelus aeneus* et *Epinephelus guaza*) de côtes de Tunisie. *Revue De Travaux Des Institut Peches Maritim, Nantes.* **39**: 313-320.

Bruslé-Sicard, S., Débas, L., Fourcault, B. and Fuchs, J. 1992. Ultrastructural study of sex inversion in a protogynous hermaphrodite, *Epinephelus microdon* (Teleostei, Serranidae). *Reproduction, nutrition, development.* **32**: 393-406.

Bullock, L.H., Murphy, M.D., Godcharles, M.F. and Mitchell, M. 1992. Age, growth and reproduction of jewfish *Epinephelus itajara* in the eastern Gulf of Mexico. *Fishery bulletin.* **90**: 243-249.

Bush, P.G., Ebanks, G.C. and Lane, E.D. 1996. Validation of aging technique for Nassau grouper (*Epinephelus striatus*) in the Cayman Islands. In: *Proceedings of an EPOMEX/ICLARM international workshop on tropical snappers and groupers.* Arreguin-Sanchez, J. Munro, M.C. Balgos and D. Pauly. Eds. 26-29 October 1993, Campeche, Mexico. pp. 150-157.

Butterworth, D.S., Punt, A.E., Borchers, D.L., Pugh, J.B., and Hughes, G.S. 1989. A manual of mathematical techniques for linefish assessment. *South African national scientific programmes report.* **160**: 1-89.

Buxton, C.D. 1987. Life history changes of two reef fish species in exploited and unexploited marine environments in South Africa. Unpublished PhD thesis, Rhodes University, Grahamstown. 220 pp.

Buxton, C.D. 1990. Problems associated with the management of line fishes. In: Marine recreational fishing: resource usage, management and research. van der Elst, R. Ed. *South African national scientific programmes report.* **167**: 41-45.

Buxton, C.D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. *Fisheries research.* **15**: 1-16.

Buxton, C.D. 1993. Life history changes in exploited reef fishes on the east coast of South Africa. *Environmental biology of fishes.* **36**: 47-63.

Buxton, C.D. and Clarke, J.R. 1986. Age, growth and feeding of the blue hottentot *Pachymetopon aeneum* (Pisces: Sparidae) with notes on reproductive biology. *South African journal of zoology.* **21**: 33-38.

Buxton, C.D. and Clarke, J.R. 1989. The growth of *Cymatoceps nasutus* (Teleostei: Sparidae) with comments on diet and reproduction. *South African journal of marine science.* **8**: 57-65.

Caddy, J.F. and Mahon, R. 1995. Reference points for fisheries management. *FAO Fisheries Technical paper.* **347**: 83 pp.

Campana, S.E. and Neilson, J.D. 1985. Microstructure of fish otoliths. *Canadian journal of fisheries and aquatic sciences.* **42**: 1014-1032.

Chale-Matsau, J.R., Govender, A. and Beckley, L.E. (in press). Age, growth and retrospective stock assessment of the economically extinct sparid fish *Polysteganus undulosus* from South Africa. *Fisheries research.* **1109**.

Chan, S.T.H. and Yeung, W.S.B. 1983. Sex control and sex reversal in fish under natural conditions. In: *Fish Physiology* IX. Hoar, W.S., Randall, D.J. and Donaldson, E.M. Eds. Academic Press, New York. pp. 171-222.

Charnov, E.L. 1982. *The theory of sex allocation.* Princeton University Press, Princeton. 355 pp.

Chater, S.A., Beckley, L.E., Garratt, P.A., Ballard, J.A. and van der Elst, R.P. 1993. Fishes from offshore reefs in the St Lucia and Maputaland Marine Reserves, South Africa. *Lammergeyer.* **42**: 1-17.

Chater, S.A., Beckley, L.E., van der Elst, R.P. and P.A. Garratt 1995. Underwater visual census of fishes in the St Lucia marine reserve, South Africa. *Lammergeyer*. **43**: 15-23.

Chauvét, C. 1988. Etudie de la croissance du merou *Epinephelus guaza* (Linne, 1758) des côtes tunisiennes. *Aquatic living resources*. **1**: 277-288.

Chauvét, C. 1991. Statut d'*Epinephelus guaza* (Linnaeus, 1758) et elements de dynamyque des populations mediterranéen et atlantique. In: *Les espéces marines a proteger en Mediterranée*. Boudouresque, C.F., Avon, M. and Graves, V. GIS Posidonie. Eds. France. pp. 255-275.

Choat, J.H. and Robertson, D.R. 1975. Protogynous hermaphroditism in fishes of the family Scaridae. In: *Intersexuality in the animal kingdom*. Reinboth, R. Ed. Springer-Verlag, New York. pp. 263-283.

Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. *Canadian journal of fisheries and aquatic sciences*. **48**: 734-750.

Clark, W.G. 1993. The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. In: *Proceedings of the international symposium on management strategies for exploited populations*. Kruse, G., Eggers, D.M., Marasco, R.J., Patuzke, C. and Quin, T.J. Eds. Alaska Sea Grant report. **9-02**: 233-246.

Clarke, R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Marine Biology*. **40**: 277-289.

Cooke, J.G. and Beddington, J.R. 1981. Biases in estimation of natural mortality and how to avoid them. Paper SC/33/05, presented to the International Whaling Commission Scientific Committee, June 1981 (unpublished). Reported In: A manual of mathematical techniques for linefish assessment. Butterworth, D.S., Punt, A.E., Borchers, D.L., Pugh, J.B. and Hughes, G.S. Eds. 1989. *South African national scientific programmes report*. **160**: pp. 1-89.

Cole, K.S. and Shapiro, D.Y. 1990. Gonad structure and hermaphroditism in the Gobiid genus *Coryphopterus* (Teleostei: Gobiidae). *Copeia*. **1990(4)**: 996-1003.

Coleman, F.C., Koenig, C.C., and Collins, L.A. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental biology of fishes*. **47**: 129-141.

Coleman, F.C., Koenig, C.C., Eklund, A. and Grimes, C.B. 1999. Management and conservation of temperate reef fishes in the grouper-snapper complex of the southeastern United States. In: Life in the slow lane: ecology and conservation of long-lived marine animals. Musick, J.A. Ed. *American Fisheries Society Symposium*. **23**: 233-242.

Coleman, F.C., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A.M., McGovern, J.C., Chapman, R.W., Sedberry, G.R. and Grimes, C.B. 2000. Long-lived reef fishes: the snapper-grouper complex. *Fisheries.* **25(3)**: 14-21.

Colin, P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental biology of fishes.* **34**: 357-377.

Colin, P.L., Shapiro, D.Y. and Weiler, D. 1987. Aspects of the reproduction of two species of groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. *Bulletin of marine science.* **40**: 220-230.

Collins, A.L., Johnson, A.G., Koenig, C.C., and Baker, M.S. 1998. Reproductive patterns, sex ratio, and fecundity in the gag, a protogynous grouper (Serranidae: *Mycteroperca microlepis*) from the northeastern Gulf of Mexico. *Fishery bulletin.* **96**: 415-427.

Conover, D.O. 1992. Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology.* **41**: Supplement B, 161-178.

Cordes, J.F. and Allen, L.G. 1997. Estimates of age, growth and settlement from otoliths of young-of-the-year kelp bass (*Paralabrax clathratus*). *Bulletin of the Southern California Academy of Sciences.* **96(2)**: 43-60.

Craig, M.T., Pondella, D.J. and Hafner, J.C. 1999. Analysis of age and growth in two eastern Pacific groupers (Serranidae: Epinephelinae). *Bulletin of marine science.* **65(3)**: 807-814.

Crowder, L.B., Lyman, S.J., Figueira, W.F. and Priddy, J. 2000. Source-sink population dynamics and the siting of marine reserves. *Bulletin of Marine Science.* **66**(3): 799-820.

Csirke, J., Caddy, J.F. and Garcia, S. 1985. Methods of size frequency analysis and their incorporation in programs for fish stock assessment in developing countries. In: Length-based methods in fisheries research. Pauly, D. and Morgan, G.R. Eds. *Proceedings of the international conference on the theory and application of length-based methods for stock assessment,* 11-16 February 1985, Sicily, Italy. pp. 1-6.

Cushing, D.H. 1983. *Key papers on fish populations.* IRL Press, Oxford. 405 pp.

Darwall W.R.T., Costello, M.J., Donnelly, R. and Lysaght, S. 1992. Implications of life history strategies for a new wrasse fishery. *Journal of Fish Biology.* **41(B)**: 111-124.

De Vlamming, V., Grossman, G. and Chapman, F. 1982. On the use of the gonosomatic index. *Comparative biochemistry and physiology.* **73A(1)**: 31-39.

Doherty, P.J. 1991. Spatial and temporal patterns in recruitment. In: *The ecology of fishes on coral reefs.* Sale, P.F. Ed. Academic Press, San Diego. pp. 261-293.

Domeier, M.L. and Colin, P.L. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of marine science.* **60(3)**: 698-726.

Draper, N.R. and Smith, H. 1966. *Applied Regression Analysis.* Wiley, New York. 709 pp.

Efron, B. 1981. Nonparametric estimates of standard error: the jacknife, the bootstrap and other methods. *Biometrika.* **68(3)**: 589-599.

FAO. 1998. FAO yearbook. Fishery statistics - capture production. **82**: 678 pp.

Francesconi, K. and Clayton, D. 1996. Shark Bay World Heritage Property. Management paper for fish resources. Fisheries management paper. Fisheries Department (Western Australia). **91**: 1-118.

Fennessy, S.T. and Radebe, P.V. 2000. Serranidae. In: Southern African marine linefish status reports. Mann, B.Q. Ed. *Special Publication, Oceanographic Research Institute.* **7**: 111-120.

Ferreira, B.P. and Russ, G.R. 1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacepede 1802) from Lizard Island, northern Great Barrier Reef. *Fishery bulletin.* **92(1)**: 46-57.

Ferreira, B.P. and Russ, G.R. 1995. Population structure of the leopard coralgrouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, central Great Barrier Reef, Australia. *Fishery bulletin.* **93(4)**: 629-642.

Fishbase. 1998. FishBase 1998 CD-Rom. ICLARM. Manila, Phillipines.

Flemming, B.W. and Hay, R. 1988 Sediment distribution and dynamics on the Natal continental shelf. In: *Coastal ocean studies off Natal, South Africa.* Schumann, E.H. Ed. Berlin, Springer-Verlag: pp. 47-80.

Francis, R.C. 1974. Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *Journal of the Fisheries Research Board of Canada.* **31**: 1539-1542.

Garcia, S.M. 1994. Precautionary principle: its implications in capture fisheries management. *Ocean and Coastal Management.* **22**: 99-125.

Garratt, P.A. 1984. The biology and fishery of *Chrysoblephus puniceus* (Gilchrist and Thompson, 1917) and *Cheimerius nufar* (Ehrenberg, 1830), two offshore sparids in Natal waters. Unpublished Msc thesis, University of Natal. 139 pp.

Garratt, P.A. 1985. The offshore linefishery of Natal: II: Reproductive biology of the sparids *Chrysoblephus puniceus* and *Cheimerius nufar*. *Investigational Report, Oceanographic Research Institute*. **63**: 1-21.

Garratt, P.A. 1993. Slinger: The final analysis? In: *Fish, fishers and fisheries. Proceedings of the second South African marine linefish symposium.* Beckley, L.E. and van der Elst R.P. Eds. Durban, 23-24 October 1992. *Special Publication, Oceanographic Research Institute*. **2**: 14-18.

Garratt, P.A. 1996. Threatened fishes of the world: *Polysteganus undulosus* Regan 1908 (Sparidae). *Environmental biology of fishes*. **45(4)**: 62.

Garratt, P.A., Govender, A. and Punt, A.E. 1993. Growth acceleration at sex change in the protogynous hermaphrodite *Chrysoblephus puniceus* (Pisces: Sparidae). *South African journal of marine science*. **13**: 187-193.

Garratt, P.A., Birnie, S.L. and Chater, S. A. 1994. The fishery for Englishman *Chrysoblephus anglicus* and Scotsman *Polysteganus praeorbitalis* (Pisces: Sparidae) in Natal, South Africa, with notes on their biology. *Unpublished Report, Oceanographic Research Institute*. **96**: 1-25.

Garrod, D.J. and Horwood, J.W. 1984. Reproductive strategies and the response to exploitation. In: *Fish reproduction - strategies and tactics*. Potts, G.W. and Wootton, R.J. Eds. Academic Press, London. pp. 367-384.

Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. *Quarterly review of biology*. **44**: 189-208.

Gilmore, R.G. and Jones, R.J. 1992. Colour variation and associated behaviour in the epinepheline groupers *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. *Bulletin of marine science*. **51**: 84-103.

Glamuzina, B., Glavic, N., Skaramuca, B. and Kozul, V. 1998. Induced sex reversal of dusky grouper, *Epinephelus marginatus* (Lowe). *Aquaculture Research*. **29**: 563-567.

Goodyear, C.P. 1988. Yield per recruit analysis for several reef fish species of the Gulf of Mexico. *A report to the Gulf of Mexico Fishery Management Council by the Miami Laboratory, Southeast Fisheries Center, NOAA, United States Department of Commerce*. CRD 87/88-14.

Goodyear, C.P. 1989. Spawning stock biomass per recruit: The biological basis for a fisheries management tool. *ICCAT Working Document*. SCRS/89/82. 10 pp.

Govender, A. 1995. Mortality and biological reference points for the king mackerel (*Scomberomorus commerson*) fishery off the coast of Natal, South Africa (based on a per-recruit assessment). *Fisheries research*. **23**: 195-208.

Grant, C. 1981. High catch rates in Norfolk Island dropline fishery. *Australian fisheries.* **40(3)**: 10-13.

Griffiths, M.H. 1996. Age and growth of South African silver kob, *Argyrosomus inodorus* (Sciaenidae), with evidence for separate stocks based on otoliths. *South African journal of marine science.* **17**: 37-48.

Griffiths, M.H. 1997a. Management of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on per-recruit models. *South African journal of marine science.* **18**: 213-228.

Griffiths, M.H. 1997b. Management objectives and strategies for the South African linefishery. In: Management and monitoring of the South African marine linefishery. Penney, A.J., Griffiths, M.H. and Attwood, C.G. Eds. *South African Network for Coastal and Oceanic Research, Occasional Report.* **3**: 3-14.

Gulland, J.A. 1968. The concept of marginal yield from exploited fish stocks. *Conseil International Pour L'Exploration de la Mer.* **32**: 256-261.

Gulland, J.A. Ed. 1971. *The fish resources of the ocean.* Fishing News Books Ltd., Surrey. 225 pp.

Gulland, J.A. 1975a. Length-based methods in fisheries research: from theory to application. In: Length-based methods in fisheries research. Pauly, D and Morgan, G.R. Eds. *Proceedings of the international conference on the theory and application of length-based methods for stock assessment,* 11-16 February 1985, Sicily, Italy. pp. 335-342.

Gulland, J.A. 1975b. Manual of sampling and statistical methods for fisheries biology. Part 1. Sampling methods. *FAO manual of fisheries science.* **3**: 87 pp.

Gulland, J.A. 1984. Best estimates. *Fishbyte.* **2(3)**: 3-5

Gulland, J.A. 1988. The problems of population dynamics and contemporary fishery management. In: *Fish population dynamics.* Gulland, J.A. Ed. John Wiley and Sons, London. pp. 383-406.

Gulland, J.A. and Rosenberg, A.A. 1992. A review of length-based approaches to assessing fish stocks. *FAO fisheries technical paper.* **323**: 1-100.

Harris, P.J. and McGovern, J.C. 1997. Changes in the life history of the red porgy, *Pagrus pagrus*, from the southeastern United States, 1972-1994. *Fishery bulletin.* **95**: 732-747.

Harris, P.J. and Collins, M.R. 2000. Age, growth and age at maturity of gag, *Mycteroperca microlepis,* from the southeastern United States during 1994-1995. *Bulletin of marine science.* **66(1)**: 105-117.

Hastings, P.A. 1989. Protogynous hermaphroditism in the genus *Paralabrax maculatofasciatus* (Pisces: Serranidae). *Copeia*. **1989**: 184-188.

Hecht, T. and Smale, M.J. 1986. In: *Proceedings of a workshop on age determination and growth modelling of South African marine linefish.* Rhodes University, Grahamstown, 10 - 12 August 1986. Grahamstown, JLB Smith Institute of Ichthyology. pp. 1-40.

Heemstra, P.C. and Randall, J.E. 1986. Family No. 166: Serranidae. In: *Smith's sea fishes.* Smith, M.M. and Heemstra, P.C. Eds. Johannesburg, Macmillan. pp. 509-637.

Heemstra, P.C. and Randall, J.E. 1993. FAO species catalogue. Vol. 16. Groupers of the world (Family Serranidae, Subfamily Epinephilinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. *FAO fisheries synopsis.* **125 (16)**: 382 pp.

Helfman, G.S. 1978. Patterns of community structure in fishes: summary and overview. *Environmental biology of fishes.* **3**: 129-148.

Henderson, P.A. and Seaby, R.M. 1999. Population stability of the sea snail at the southern edge of its range. *Journal of fish biology.* **54**: 1161-1176.

Hood, P.B, and Schlieder, R.A. 1992. Age, growth and reproduction of gag *Mycteroperca microlepis* (Pisces: Serranidae) in the eastern Gulf of Mexico. *Bulletin of marine science.* **51**: 337-352.

Hood, P.B., Godcharles, M.F. and Barco, R.S. 1994. Age, growth, reproduction, and the feeding ecology of black sea bass, *Centropristis striata* (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bulletin of marine science.* **54(1)**: 24-37.

Hunter, I.T. 1988. Climate and weather off Natal. In: *Coastal ocean studies off Natal, South Africa.* Schumann, E.H. Ed. Berlin, Springer-Verlag. pp. 81-100.

Huntsman, G.R., Manooch, C.S. and Grimes, C.B. 1983. Yield per recruit models of some reef fishes of the U.S. South Atlantic Bight. *Fishery bulletin* **81(4)**: 679-695.

Huntsman, G.R. and Waters, J.R. 1987. Development of management plans for reef fishes – Gulf of Mexico and U.S. South Atlantic. In: *Tropical snappers and groupers: biology and fisheries management.* Polovina, J.J. and Ralston, S. Eds. Westview Press, Inc., Colorado. pp. 533-560.

Huntsman, G.R. and Schaaf, W.E. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the graysby. *North American journal of fisheries management.* **14**: 41-52.

Huntsman, G.R., Potts, J., and Mays, R.W. 1994. A preliminary assessment of the populations of seven species of grouper in the western Atlantic Ocean from Cape Hatteras, North Carolina to the Dry Tortugas, Florida. In: *Proceedings of the Gulf and Caribbean Fisheries Institute.* **43**: 193-213.

Huntsman, G.R., Potts, J., Mays, R.W. and Vaughan, D. 1999. Groupers (Serranidae, Epinephelinae): Endangered apex predators of reef communities. In: *Life in the slow lane: ecology and conservation of long-lived marine animals.* Musick, J.A. Ed. American Fisheries Society Symposium. **23**: 217-232.

Jennings, S., Grandcourt, E.M. and Polunin, N.V.C. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. Special issue: Science and management. *Coral reefs.* **14(4)**: 225-235.

Jennings, S. and Lock, J.M. 1996. Population and ecosystem effects of reef fishing. In: *Reef fisheries.* Polunin, N.V.C and Roberts, C.M. Eds. Chapman and Hall, London. pp. 193-218.

Jennings, S., Reynolds, J.D. and Mills, S.C. 1998. Life history correlates of responses to fisheries exploitation. In: *Proceedings of the Royal Society of London.* **265 (1393)**: 333-339.

Jennings, S., Reynolds, J.D. and Polunin, N.V.C. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation Biology.* **13(6)**: pp. 1466-1475.

Johannes, R.E. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in ecology and evolution.* **13(6)**: 243-246.

Johannes, R.E., Squire, L., Graham, T., Sadovy, Y.[J.] and Renguul, H. 1999. Spawning arregations of groupers (Serranidae) in Palau. *The Nature Conservancy: Marine conservation series publication.* **1**: 144 pp.

Kara, M.H. and Derbal, F. 1995. Morphométrie, croissance et mortalité du Mérou *Epinephelus marginatus* (Serranidae) des côtes de l'est algérien. *Cahiers de biologie marine.* **6**: 229-237. Reported in Bouchereau et al., 1999.

Koenig, C.C., Coleman, F.C., Collins, L.A., Sadovy, Y. [J.] and Colin, P.L. 1996. Reproduction in gag (*Mycteroperca microlepis*) and the consequences of fishing spawning aggregations. In: *Proceedings of an EPOMEX/ICLARM international workshop on tropical snappers and groupers.* Arreguin-Sanchez, F., Munro, J.L., Balgos, M.C. and Pauly, D. Eds. 26-29 October 1993, Campeche, Mexico. pp. 307-323.

Lang, J.B. and Buxton, C.D. 1993. Validation of age estimates in sparid fish using fluorochrome marking. *South African journal of marine science.* **13**: 195-203.

Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. *Transactions of the American Fisheries Society*. **106(1)**: 1-11.

Lau, P.F. and Parry-Jones, R. 1999. The Hong Kong trade in live reef fish for food. TRAFFIC East Asia and World Wide Fund for Nature Hong Kong, Hong Kong. 65 pp.

Lincoln, R.J., Boxshall, G.A. and Clark, P.F. Eds. 1982. *A dictionary of ecology, evolution and systematics.* Cambridge University Press. 298 pp.

Longhurst, A.R and Pauly, D. Eds. 1987. *Ecology of tropical oceans.* San Diego; Academic Press, Inc. 407 pp.

Love, R.M. 1970. *The chemical biology of fishes (Volume 2)*: Academic Press, London. 547 pp.

Ludwig, D., Hilborn, R. and Walters, C. 1993. Uncertainty, resource exploitation and conservation. *Science*. **260(5104)**: 17,36.

Lutjeharms, J.R.E. and Roberts, H.R. 1988. The Natal Pulse: an extreme transient on the Agulhas current. *Journal of geophysical research*. **93**: 631-645.

Lutjeharms, J.R.E., Valentine, H.R. and van Ballegooyen, R.C. 2000. The hydrography and water masses of the Natal Bight, South Africa. *Continental shelf research*. **20**: 1907-1939.

Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Canadian journal of fisheries and aquatic sciences*. **51**: 110-122.

Mace, P.M. 1999. Current status and prognosis for marine capture fisheries. *Fisheries*. **24(3)**: 30.

Mace, P.M. and Sissenwine, M.P. 1993. How much spawning per recruit is enough? In: Risk evaluation and biological reference points for fisheries management. *Canadian special publication of fisheries and aquatic sciences*. **120**: 101-118.

Mackie, M. 1998. Biology and ecology of the chinaman cod, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. PhD thesis, University of Western Australia. 177 pp.

Mackie, M. 2000. Reproductive biology of the halfmoon grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. *Environmental biology of fishes*. **57**: 363-376.

Macpherson, E. and Duarte, C.M. 1991. Bathymetric trends in demersal fish size: is there a general relationship? *Marine ecology progress series*. **71**: 103-112.

Malan, O.G. and Schumann, E.H. 1979. Natal shelf circulation revealed by Landsat imagery. *South African journal of science.* **75**: 136-138.

Mann, B.Q. Ed. 2000. Southern African marine linefish status reports. *Special Publication, Oceanographic Research Institute.* **7**: 257 pp.

Mann B.Q. and Buxton, C.D. 1997. Age and growth of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Sparidae) on the Tsitsikamma coast, South Africa. *Cybium.* **21(2)**: 135-147.

Mann, B.Q., Beckley, L.E. and van der Elst, R.P. 1997 Evaluation of linefishery participation and management along the KwaZulu-Natal coast. *Unpublished Report, Oceanographic Research Institute.* **134**: 1-17.

Mann, B.Q. and Radebe, P.V. 2000. *Rhabdosargus sarba*. In: Southern African marine linefish status reports. Mann, B.Q. Ed. *Special Publication, Oceanographic Research Institute.* **7**: 184-186.

Manooch, C.S. 1982. Ageing of fishes in the Southeast Fisheries Center. In: Proceedings of a workshop held October 7-10 1980, St Thomas, Virgin Islands. G.R. Huntsman, W.R. Nicholson and W.W. Fox. Jr. Eds. *NOAA technical memorandum NMFS SEFC.* **80**: 24-43.

Manooch, C.S. 1987. Age and growth of snappers and groupers. In: *Tropical snappers and groupers: biology and fisheries management.* Polovina, J.J. and Ralston, S. Eds. Westview Press, Inc., Colorado. pp. 329-373.

Manooch, C.S. and Mason, D.L. 1987. Age and growth of the warsaw grouper and black grouper from the southeast region of the United States. *Northeast Gulf science.* **9(2)**: 65-75.

Marine and Coastal Management. 1997. Unpublished reports. Department of Environmental Affairs and Tourism.

Marine Reserves Task Group. 1997. Towards a new policy on marine protected areas for South Africa. *South African Network for Coastal and Oceanic Research, Occasional Report.* **2**: 127 pp.

Martin, A.K. and Flemming, B.W. 1988 Physiography, structure and geological evolution of the Natal continental shelf. In: *Coastal ocean studies off Natal, South Africa.* Schumann, E.H. Ed. Berlin, Springer-Verlag. pp. 11-46.

Matheson, R.H. and Huntsman, G.R. 1984. Growth, mortality and yield-per-recruit models for the speckled hind and snowy grouper from the United States south Atlantic bight. *Transactions of the American Fisheries Society.* **113**: 607-616.

Mathews, C.P. and Samuel, M. 1987. Growth, mortality and assessments for groupers from Kuwait. *Kuwait bulletin of marine science.* **9**: 173-191.

McGovern J.C., Wyanski, D.M., Pashuk, O., Manooch, C.S. and Sedberry, G.R. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, form the Atlantic coast of the southeastern United States during 1976-1995. *Fishery bulletin.* **96(4)**: 797-807.

Miranda, L.E., Wingo, W.M., Muncy, R.J. and Bates, T.D. 1987. Bias in growth estimates derived from fish collected by anglers. In: *Age and growth of fish.* Summerfelt, R.C. and Hall, G.E. Eds. Iowa State University Press, Ames, IA. pp. 211-220.

Moe, M.A. 1969. Biology of the red grouper *Epinephelus morio* (Valenciénnes) from the eastern Gulf of Mexico. *Florida Department of Natural Resources, Marine Research Laboratory: Professional papers series.* **No. 10**: 1-95.

Moreau, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. In: *Age and growth of fish.* Summerfelt, R.C. and Hall, G.E. Eds. Iowa State University Press, Ames, IA. pp. 81-113.

Morgans, J.F.C. 1964. A preliminary fishery survey of bottom fishing on the north Kenya Banks. *Colonial Office (London). Fishery Publications.* **21**: 1-64

Morgans, J.F.C. 1982. Serranid fishes of Tanzania and Kenya. *Ichthyological Bulletin, J.L.B. Smith Institute of Ichthyology.* **46**: 33 pp.

Munro, J.L. Ed. 1983. Caribbean coral reef fishery resources. *ICLARM studies and reviews.* **7**: 276 pp.

Nelder, J.A. and Mead, R. 1965. A simplex method for function minimisation. *Computer Journal.* **7**: 308-313.

Nzioka, R.M. 1979. Observations on the spawning seasons of East African reef fishes. *Journal of fish biology.* **14**: 329-342.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil. Conseil international pour l'Exploration de la Mer.* **39(3)**: 175-192.

Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung.* **28(4)**: 251-282.

Pauly, D. 1983. Some simple methods for the assessment of tropical fish stocks. *FAO fisheries technical paper.* **234**: 52 pp.

Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM, Manila. 325 pp.

Pauly, D. and Binohlan, C. 1996. Fishbase and AUXIM as tools for comparing life-history patterns, growth and natural mortality of fish: applications to snappers and groupers. In: *Proceedings of an EPOMEX/ICLARM international workshop on tropical snappers and groupers.* Arreguin-Sanchez, F., Munro, J.L., Balgos, M.C. and Pauly, D. Eds. 26-29 October 1993, Campeche, Mexico. pp. 218-243.

Penney, A.J. 1997 The National Marine Linefish System: A decade in review. In: Management and monitoring of the South African marine linefishery. Penney, A.J., Griffiths, M.H. and Attwood, C.G. Eds. *South African Network for Coastal and Oceanic Research, Occasional Report.* **3**: 23-50.

Penney, A.J., Griffiths, M.H. and Attwood, C.G. Eds. 1997. Management and monitoring of the South African marine linefishery. *South African Network for Coastal and Oceanic Research, Occasional Report.* **3**: 87 pp.

Penney, A.J., Mann-Lang, J.B., van der Elst, R.P. and Wilke, C. 1999. Long term catch and effort trends in the KwaZulu-Natal offshore commercial and receational linefisheries. *South African journal of marine science.* **21**: 51-76.

Pianka, E.R. 1974. *Evolutionary ecology.* New York: Harper and Row. 356 pp.

Pitcher, T.J. and Hart, P.J.B. Eds. 1982. *Fisheries Ecology.* Croom Helm, London. 414 pp.

Pitcher, T.J. and Pauly, D. 1998. Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. Eds. Fish and fisheries series **23**. Kluwer Academic Publishers, Dordrecht. pp. 311-330

Pitcher, T.J., Bundy, A., Preikshot, D., Hutton, T. and Pauly, D. 1998. Measuring the unmeasurable: a multivariate and interdisciplinary method for rapid appraisal of the health of fisheries. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. Eds. Fish and fisheries series **23**. Kluwer Academic Publishers, Dordrecht. pp. 31-54.

Plan Development Team. 1990. The potential for marine fishery reserves for reef fish management in the U.S. southern Atlantic. Coastal Resources Division, Contribution No. CRD/89-90/04.

Pollock, B.R. 1984. Relations between migration, reproduction and nutrition in yellowfin bream *Acanthopagrus australis. Marine ecology progress series.* **19**: 17-23.

Potts, J.C. and Manooch, C.S. 1995. Age and growth of red hind and rock hind collected from North Carolina through the Dry Tortugas, Florida. *Bulletin of marine science.* **56(3)**: 784-794.

Potts, J.C. and Manooch, C.S. 1999. Observations on the age and growth of graysby and coney from the souheastern United States. *Transactions of the American Fisheries Society.* **128**: 751-757.

Powell, D.G. 1979. Estimation of mortality and growth parameters from the length-frequency in the catch. *Rapport et proces-verbaux des reunions. Conseil international pour l'Exploration de la Mer.* **175**: 167-169.

Pulliam, H.R. 1988. Sources, sinks and population regulation. *American Naturalist.* **132**: 652-661.

Punt, A.E. 1992. PC-YIELD II User's guide (version 2.2). *Reports of the Benguela ecology programme of South Africa.* **26**: 1-36.

Punt, A.E. 1993. Use of spawner-biomass-per-recruit in the management of linefisheries. In: *Fish, Fishers and Fisheries. Proceedings of the second South African marine linefish symposium.* Beckley, L.E. and van der Elst R.P. Eds. Durban, 23-24 October 1992. *Special Publication, Oceanographic Research Institute.* **2**: 80-89.

Punt, A.E. and Hughes, G.S. 1989. PC-Yield II user's guide. *Reports of the Benguela ecology programme of South Africa.* **18**: 1-60.

Punt, A., Garratt, P.A., and Govender, A. 1993. On an approach for applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysoblephus puniceus* (Pisces: Sparidae). *South African journal of marine science.* **13**:109-119.

Rafail, S.Z., Daoud, W.L. and Hilal, M.M. 1969. Longline Mediterranean fisheries studies west of Alexandria. *CGPM Etud. Rev.* **42**: 3-16. Reported in Bouchereau *et al.*, 1999.

Ralston, S. 1987. Mortality rates of tropical snappers and groupers. In: *Tropical snappers and groupers: biology and fisheries management.* Polovina, J.J. and Ralston, S. Eds. Westview Press, Inc., Colorado. pp 375-404.

Reinboth, R. 1967. Biandric teleost species. *General and comparative endocrinology.* **9**: Abstract number 146.

Reinboth, R. 1970. Intersexuality in fishes. *Memoirs of the Society for Endocrinology.* **18**: 515-543

Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *Journal of the Fisheries Research Board of Canada.* **26**: 478-541.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada.* **191**: 382 pp.

Ricker, W.E. 1979. Growth rates and models. In: *Fish physiology III: Bioenergetics and growth.* Hoar, W.S., Randall, D.J. and Brett, J.R. Eds. Academic Press, New York. pp. 677-743.

Rikhter, V.A. and Efanov, V.A. 1977. On one of the approaches of estimating natural mortality of fish populations. *Trudy Atlanticheskogo nauchno-issledovatel' skogo instituta rybnogo khozyajstva I okeanografii.* **73**: 77-85.

Robertson, D.R. and Warner, R.R. 1978. Sexual patterns in the labroid fishes of the western Caribbean, II. The parrotfishes (Scaridae). *Smithsonian contributions to zoology.* **255**: 1-26.

Ross, R.M. 1990. The evolution of sex-change mechanisms in fishes. *Environmental biology of fishes.* **29**: 81-93.

Ruddle, K. 1996. Geography and human ecology of reef fisheries. In: *Reef fisheries.* Polunin, N.V.C. and Roberts, C.M. Eds. Chapman and Hall, London. pp. 137-160.

Russ, G.R. 1991. Coral reef fisheries: effects and yields. In: *The ecology of fishes on coral reefs.* Sale, P.F. Ed. Academic Press Inc., Florida. pp. 601-635.

Sadovy, Y. [J.] 1994. Grouper stocks of the western central Atlantic: the need for management and management needs. In: *Proceedings of the Gulf and Caribbean Fisheries Institute.* **43**: 43-64.

Sadovy, Y. [J.] 1996. Reproduction of reef fishery species. In: *Reef fisheries* Polunin, N.V.C. and Roberts, C.M. Eds. Chapman and Hall, London. 15-60.

Sadovy, Y. [J.] and Shapiro, D.Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia.* **1987(1)**: 136-156.

Sadovy, Y.[J.] and Figuerola, M. 1989. The status of the red hind fishery in Puerto Rico and St Thomas as determined by yield-per-recruit analysis. In: *Proceedings of the Gulf and Caribbean Fisheries Institute.* **42**: 23-38.

Sadovy, Y. [J.], Figuerola, M. and Román, A. 1992. Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St Thomas. *Fishery bulletin.* **90**: 516-528.

Sadovy, Y. [J.], Colin, P.L. and Domeier, M.L. 1994. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). *Copeia.* **1994(2)**: 511-516.

Sadovy, Y. [J.], Rosario, A. and A. Román. 1994. Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus. Environmental biology of fishes.* **41**: 269-286.

Sadovy, Y. [J.] and Colin, P.L. 1995. Sexual development and sexuality in the Nassau grouper. *Journal of fish biology.* **46**: 961-976.

Sauer, W.H.H., Penney, A.J., Erasmus, C., Mann, B.Q., Brouwer, S.L., Lamberth, S.J., and Stewart, T.J. 1997a. An evaluation of attitudes and responses to monitoring and management measures for the South African boat-based linefishery. *South African journal of marine science.* **18**: 147-163.

Sauer, W.H.H., Mann, B.Q., Brouwer, S.L., and Lamberth, S.J., 1997b. An evaluation of participation in, and management of, the South African linefishery. In: Management and monitoring of the South African marine linefishery. Penney, A.J., Griffiths, M.H. and Attwood, C.G. Eds. *South African Network for Coastal and Oceanic Research, Occasional Report.* **3**: 51-56.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Canadian journal of fisheries and aquatic sciences.* **38**: 1128-1140.

Schumann, E.H. 1982. Inshore circulation of the Agulhas current off Natal. *Journal of marine research.* **40**: 43-55.

Schumann, E.H. 1988. Physical oceanography off Natal. In: *Coastal ocean studies off Natal, South Africa.* Schumann, E.H. Ed. Berlin, Springer-Verlag. pp. 101-131

Shannon, L.V. 1989. The physical environment. In: *Oceans of life off southern Africa.* Payne, A.I.L. and Crawford, R.J.M. Vlaeberg. Eds. Publishers, Cape Town. pp. 12-27.

Shapiro, D.Y. 1984. Sex reversal and sociodemographic process in coral reef fishes. In: *Fish reproduction. Strategies and tactics.* Potts, G.W. and Wootton, R.J. Eds. Academic Press, London, England. pp. 103-118

Shapiro, D.Y. 1987. Reproduction in groupers. In: *Tropical snappers and groupers: biology and fisheries management.* Polovina, J.J. and Ralston, S. Eds. Westview Press, Inc., Colorado. pp. 295-28.

Shapiro, D.Y. 1988. Behavioural influences on gene structure and other new ideas concerning sex change in fishes. *Enviromental biology of fishes.* **23**: 283-297

Shapiro, D.Y., Sadovy, Y. [J.] and McGehee, M.A. 1993a. Size, composition and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). *Copeia.* **1993(2)**: 399-406.

Shapiro, D.Y., Sadovy, Y. [J.] and McGehee, M.A. 1993b. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bulletin of marine science.* **53(3)**: 1151-1162.

Sheaves, M. 1995. Large lutjanid and serranid fishes in tropical estuaries: Are they adults or juveniles? *Marine ecology progress series.* **129**: 31-40.

Sheperd, G.R. and Idoine, J.S. 1993. Length-based analyses of yield and spawning biomass per recruit for black sea bass *Centropristis striata*, a protogynous hermaphrodite. *Fisheries Bulletin*. **91**: 328-337.

Siau, Y. 1994. Population structure, reproduction and sex-change in a tropical east Atlantic grouper. *Journal of fish biology*. **44**: 205-211.

Siems, D.P. and Sikes, R. 1998. Tradeoffs between growth and reproduction in response to temporal variation in response to temporal reduction in food supply. *Enviromental biology of fishes*. **53**: 319-329.

Smale, M.J. and Punt, A.E. 1991. Age and growth of the red steenbras *Petrus repestris* (Pisces: Sparidae) on the south-east coast of South Africa. *South African journal of marine science*. **10**: 131-139.

Smith, C.L. 1959. Hermaphroditism in some serranid fishes from Bermuda. *Papers. Michigan Academy of Science, Arts and Letters*. **44**: 111-119.

Smith, C.L. 1965. The patterns of sexuality and the classification of serranid fishes. *American museum novitates*. **2207**: 1-20.

Smith, C.L. 1967. Contribution to the theory of hermaphroditism. *Journal of theoretical biology*. **17**: 76-90.

Smith, C.L. 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Transactions of the American Fisheries Society*. **101**: 257-261.

Smith, C.L. 1975. The evolution of hermaphroditism in fishes. In: *Intersexuality in the animal kingdom*. Reinboth.R. Ed. Springer-Verlag, Berlin Germany. pp. 295-310.

Smith, C.L. 1982. Patterns of reproduction in coral reef fishes. In: The biological bases for reef fishery management. Huntsman, G.R., Nicholson, W.R. and Fox, J.J. Eds. *United States Department of Commerce. NOAA technical memorandum NMFS-SEFC*. **80**: 49-66.

Smith, C.L. and Young, P.H. 1966. Gonad structure and the reproductive cycle of the kelp bass, *Paralabrax clathratus* (Girard) with comments on the relationships of the serranid genus *Paralabrax*. *California fish and game*. **52(4)**: 283-292.

Sparre, P. and Venema, S.C. 1998. Introduction to tropical fish stock assessment. *FAO fisheries technical paper*. **306/1(A)**: 1-212.

Spedicato, M.T., Lembo, G., Di Marco, P. and Marino, G. 1995. Preliminary results in the breeding of dusky grouper *Epinephelus marginatus* (Lowe, 1834). *Cahiers Options Mediterranéens*. **16**: 131-148.

Staunton-Smith, J., Blaber, S.J.M. and Greenwood, J.G. 1999. Interspecific differences in the distribution of adult and juvenile ponyfish (Leiognathidae) in the Gulf of Carpentaria, Australia. *Marine and freshwater research*. **50(7)**: 643-654.

Stearns, S.C. 1992. *The evolution of life histories.* Oxford University Press, Oxford. 249 pp.

Steffe, A.S. and Murphy, J.J. 1995. A survey of recreational trailer boat fishing in the marine waters of New South Wales - a case study. In: *Recreational fishing - what's the catch?* Hancock, D.A. Ed. Workshop proceedings, Australian Society for Fish Biology. Canberra 30-31 August 1994.

Stolzenberg, W. 1994. Curiosity killed the grouper. *Sea Frontiers.* **40(2)**: 20-21.

Tanaka, H., Hirose, K., Nogami, K., Hattori, K.and Ishibashi, N. 1990. Sexual maturation and sex reversal in red spotted grouper *Epinephelus akaara. Bulletin of the National Research Institute of Aquaculture (Japan).* **17**: 1-15.

Thompson, G.G. 1993. A proposal for a threshold stock size and maximum mortlaity rate. *Canadian special publication of fisheries and aquatic sciences.* **120**: 303-320.

Thompson, R. and Munro, J.L. 1983. The biology, ecology and bionomics of the hinds and groupers, Serranidae. In: *Caribbean coral reef fishery resources.* Munro, J.L. Ed. *ICLARM studies and reviews.* **7**: 59-81.

Thresher, R.E. 1984. *Reproduction in reef fish.* Neptune City; T.F.H. Publications. pp. 68-74.

Tilney, R.L. 1990. Aspects of the biology, ecology and population dynamics of *Galeichthys feliceps* (Valenciennes) and *G. ater* (Castelnau) (Pisces: Ariidae) off the south-east coast of South Africa. Unpublished PhD thesis, Rhodes University, Grahamstown, South Africa. 278 pp.

United Nations. 1995. Draft agreement for the implementation of the provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks. United Nations Conference on Straddling Fish Stocks and Highly Migratory Fish Stocks, fifth session, 27 March-12 April, New York. 37 pp.

Valentine, H.R., van Ballegooyen, R.C. and Lutjeharms, J.R.E. 1991. Data report on the Natal Bight Cruise, july 1989. CSIR Report EMA-D 9107. 15 pp.

Van der Elst, R.P. 1988. The shelf ichthyofauna of Natal. In: *Coastal ocean studies off Natal, South Africa.* Schumann, E.H. Ed. Berlin, Springer-Verlag. pp. 214-229.

Van der Elst, R.P. and Garratt, P.A. 1984. Draft management proposals for the Natal deep reef fishery. *Unpublished Report, Oceanographic Research Institute.* **36**: 1-31.

Van der Elst, R.P. and Adkin, F. 1991. Marine linefish: Priority species and research objectives in Southern Africa. *Special Publication, Oceanographic Research Institute.* **1**: 1-132.

Van der Elst, R.P., Govender, A. and S.A. Chater. 1993. The biology and status of the garrick (*Lichia amia*). In: *Fish, Fishers and Fisheries. Proceedings of the second South African marine linefish symposium.* Beckley, L.E. and van der Elst R.P. Eds. Durban, 23-24 October 1992. *Special Publication, Oceanographic Research Institute.* **2**: 28-31.

Van der Elst, R.P., David, B. and Govender, A. 1994. The marine linefish resources of Mozambique (status, developments and future research). *Unpublished Report, Oceanographic Research Institute.* **104**: 1-28.

Van der Walt, B.A. and Govender, A. 1996. Stock assessment of *Sarpa salpa* (Pisces: Sparidae) off the KwaZulu-Natal coast, South Africa. *South African journal of marine science.* **17**: 195-204.

Vincent, A. and Sadovy, Y. [J.] 1998. Reproductive ecology in the Conservation and Management of Fishes. In: *Behavioral Ecology and Conservation Biology.* Caro, T. Ed. Oxford University Press, New York. pp. 209-245.

Wallace, J.H. and van der Elst, R.P. Eds. 1983. Marine linefish programme priority species list. *South African National Scientific Programmes Report.* **70**: 1-113.

Walters, C. 1998. Designing fisheries management systems that do not depend upon accurate stock assessment. In: *Reinventing fisheries management.* Pitcher, T.J., Hart, P.J.B. and Pauly, D. Eds. Fish and fisheries series **23**. Kluwer Academic Publishers, Dordrecht. pp. 279-288.

Walters, C. and Pearse, P.H. 1996. Stock information requirements for quota management systems in commercial fisheries. *Reviews in fish biology and fisheries.* **6**: 21-42.

Warner, R.R. 1975. The adaptive significance of sequential hermaphroditism in animals. *American naturalist.* **109**: 61-82.

Warner, R.R. 1984. Mating behaviour and hermaphroditism in coral reef fishes. *American scientist.* **72**: 128-136.

Warner, R.R. 1988. Sex change and the size-advantage model. *Trends in ecology and evolution.* **3(6)**: 133-136.

Warner, R.R. and Robertson, D.R. 1978. Sexual patterns in the labroid fishes of the western Caribbean, I. The wrasses (Labridae). *Smithsonian contributions to zoology*. **254**: 1-27.

Waters, J.R. and Huntsman, G.R. 1986. Incorporating mortality from catch and release into yield-per-recruit analyses of minimum size limits. *North American journal of fisheries management*. **6**: 463-471.

Wenner, C.A., Roumillat, W.A. and Waltz, C.W. 1986. Contribution to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. *Fishery bulletin*. **84**: 723-741.

Wetherall, J.A., Polovina, J.J. and Ralston, S. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data. In: *ICLARM conference proceedings*. **13**: 533-74.

Williams, H.A. and Lowe, M.K. 1997. Growth rates of four Hawaiian deep slope fishes: A comparison of methods for estimating age and growth from otolith microincrement widths. *Canadian journal of fisheries and aquatic sciences*. **54(1)**: 126-136.

Williams, T. and Bedford, B.C. 1974. The use of otoliths for age determination. In: *The ageing of fish*. Bagenal, T.B. Ed. Unwin Brothers, England. pp. 114-123.

Wilson, R.R. and Burns, K.M. 1996. Potential survival of released groupers caught deepr than 40 m based on shipboard and in-situ observations, and tag-recapture data. *Bulletin of marine science*. **58(1)**: 234-247.

Wootton, R.J. 1990. *Ecology of teleost fishes*. Chapman and Hall, London. 404 pp.

Wright, A. and Richards, A.H. 1985. A multispecies fishery associated with coral reefs in the Tigak Islands, Papua New Guinea. *Asian marine biology*. **2**: 69-84.

Wyanski, D.M., Byron White, D and Barans, C.A. 2000. Growth, population age struture and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. *Fishery bulletin*. **98**: 198-218.

Zabala, M., Garcia-Rubes, A., Louisy, P. and Sala, E. 1997a. Spawning behaviour of the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). *Scientia marina*. **61(1)**: 65-77.

Zabala, M., Louisy, P., Garcia-Rubes, A., and Gracia, V. 1997b. Socio-behavioural context of reproduction in the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces, Serranidae) in the Medes Island Marine Reserve (NW Mediterranean, Spain). *Scientia marina*. **61(1)**: 79-89.

Zar, J.H. 1974. *Biostatistical analysis*. Prentice-Hall, New York. 620 pp.

Appendix 1. Results of the questionnaire used for commercial skiboat skippers who fish in the northern sampling area of KwaZulu-Natal (May and June 2000).

Only skippers from the northern sampling area were interviewed, as two of the four species investigated showed no sign of spawning south of Durban. Only skippers who had been fishing for more than 10 years were interviewed. The questions asked were:

1. Number of years spent skiboat fishing?
2. Are there certain times of the year that you catch more rockcod (i.e serranids)? When, which species, are they full of eggs? Does this happen on a particular reef or in a particular area?
3. Do you think that under-sized (sub-legal) rockcod survive when released?
4. Have you seen changes in the relative numbers of rockcod in catches over the years (which species)?
5. Have you seen changes in the sizes of rockcod caught over the years (which species)?

Seven skippers were interviewed. Their answers are summarised as follows:

Question 1
The number of years experience ranged from 12 - 28 years.

Question2
Answers varied. Five skippers said that catches increased in summer, with two indicating greater catches of *E. andersoni* in November. One said that catches of *E. albomarginatus* increased in April, when the weather was more stable and they could fish on deeper reefs. The two remaining skippers said that there was no particular seasonality, and that water currents determined where they fished and hence how much they caught. None of the skippers was able to indicate whether the fish caught at these times were gravid or not. Only two skippers gave an indication of areas in which rockcod were more commonly caught.

Question 3
Answers varied. Three skippers felt that beyond about 30m water depth, survival was poor. Two others said that water depths beyond 50m and 70m would reduce survival, while the remaining two skippers were not specific, saying that survival was possible if the fish were treated well.

Question 4
Four skippers said that catches of *E. marginatus* and/or *E. albomarginatus* had declined, and three said that there had been no change.

Question 5
Two skippers said that the mean size of *E. marginatus* and/or *E. albomarginatus* had declined, three said there had not been much change, and two said that there had been a decline in sizes of all rockcod caught.

Appendix 2: Tagging of serranids in KwaZulu-Natal

Over 4 000 individual taggers belong to the ORI/Sedgwicks/WWF tagging programme, a national initiative operating in southern Africa and co-ordinated by the Oceanographic Research Institute (PO Box 10712, Marine Parade, 4056, South Africa). Tagging of fish is undertaken by volunteer anglers while fishing recreationally, and by scientists in structured tag and release programmes. The programme commenced in 1984, and has provided valuable complementary information for stock assessments and other management procedures for several species of fish. A synopsis of tagging information on the four species of serranids investigated in this thesis is presented here.

Table 2(A).1: Summary of tagging information for four species of serranids in KwaZulu-Natal, from October 1984 to August 2000.

Species	Number tagged	Number recaptured (% in brackets)	Average time at liberty (days)	Maximum time at liberty (days)	Average distance moved (km)	Maximum distance moved (km)
E. andersoni	489	74 (15.1)	228	2 867	7	143
E. marginatus	278	40 (14.4)	247	1 736	6	92
E. rivulatus	61	5 (8.2)	106	448	<1	<1
E. albomarginatus	5	0	-	-	-	-

The high percentage of recaptures for *E. andersoni* and *E. marginatus* indicate that there is a high degree of site fidelity, complemented by the low average distances moved from the release site. There was very little indication of migration of *E. andersoni* from south to north (Table 2(A).2).

Table 2(A).2: Summary of distances and directions moved by recaptured *E. andersoni* in KwaZulu-Natal from October 1984 to August 2000. Of the 74 tagged individuals, 57 were recaptured <1 km from where they were released.

Distance moved (km)	Direction moved (no. of fish)	
	North – South	South – North
0 - 10	6	2
11 – 20	1	-
21 – 30	1	2
31 – 40	2	-
41 – 50	1	-
> 50	1	1

The numbers of fish which were measured both at the time of release and on recapture was low, hence this information was not used to validate the length at age estimates obtained from otoliths.

Appendix 3: The Powell-Wetherall method of estimating Z.

Beverton and Holt (1956) showed that :

$$Z = k * \frac{L\infty - \bar{L}}{\bar{L} - L'}$$

where: k and $L\infty$ are parameters from the special von Bertalanffy growth model;
$\bar{L}$ is the mean length of fish $\geq L'$ and
L' is "some length for which all fish of that length and longer are under full exploitation".

Subsequently, Powell (1979) and Wetherall *et al.* (1987) suggested that, as L' can assume any value greater than and equal to the smallest length at full exploitation, the Beverton and Holt (1956) equation can be used to produce a series of estimates of Z, one for each value of L' (Sparre and Venema, 1998). The Beverton and Holt (1956) equation therefore becomes a regression, with L' as the independent variable:

$$\bar{L} - L' = a + b*L'$$

and $$\frac{Z}{k} = \frac{-(1+b)}{b}$$

So by plotting $\bar{L} - L'$ against L' (Table 3(A).1, Figure 3(A).1), b can be estimated from the slope of the regression of the straight line portion of the curve, and, by substituting k from the von Bertalanffy growth model, Z can be estimated (Table 3(A).2).

Table 3(A).1: *E. rivulatus* data (all lengths) used in the Powell-Wetherall method for estimating Z. Values in bold were used for the estimation of the regression slope.

		Northern area			Southern area		
Length class (TL mm)	L'	No.	$\bar{L}$	$\bar{L} - L'$	No.	$\bar{L}$	$\bar{L} - L'$
220-240	220	9	305	85	-	-	-
240-260	240	22	307	67	3	336	96
260-280	260	28	313	53	12	337	77
280-300	280	54	319	39	39	339	59
300-320	300	55	**329**	**29**	47	345	45
320-340	320	33	**346**	**26**	**58**	**353**	**35**
340-360	340	17	**364**	**24**	**65**	**365**	**25**
360-380	360	13	**374**	**14**	**36**	**379**	**19**
380-400	380	7	**389**	**9**	**19**	**396**	**16**
400-420	400	-	-	-	**10**	**410**	**10**
420-440	420	-	-	-	1	435	15

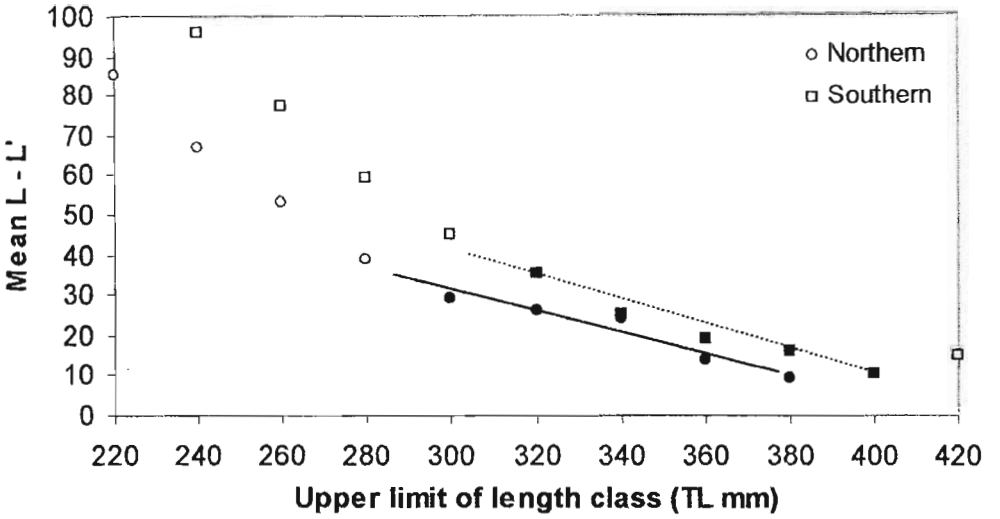


Figure 3(A).1: Powell-Wetherall plot for *E. rivulatus* based on data from Table 3.(A).1. Solid points were used for the regression lines (solid line - northern; dashed line - southern). The last data point for the southern area was excluded as it was represented by one fish.

Table 3(A).2: Results of the regressions fitted to the plot of $\bar{L} - L'$ against L' for *E. rivulatus*, with derived estimates of Z.

	Northern area	Southern area
Regression	$\bar{L} - L' = 108.8+(-0.206)*L'$	$\bar{L} - L' = 127.2+(-0.295)*L'$
r^2	0.935	0.962
Slope b	-0.206	-0.295
Z/k	2.846	2.39
k	0.394	0.477
Z	1.121	1.14
M	0.746	0.864
F	0.375	0.276

The model assumes that recruitment is continuous and that exploitation occurs over a long period. The latter is met for *E. rivulatus*, while combining samples throughout the year approximates the former assumption (Appeldoorn, 1996).